MYCOLOGIA

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

VOL. XXXIX JULY–AUGUST, 1947 NO. 4

THREE NEW SPECIES OF ZOÖPAGE PREDACEOUS ON TERRICOLOUS RHIZOPODS

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(WITH 7 FIGURES)

The genus *Zoöpage* was erected to include zygomycetous forms that in their vegetative stage capture microscopic animals through adhesion to aseptate mycelial hyphae, and that in their asexual reproductive stage give rise to chains of aerial conidia. Its predaceous mycelial habit, though not its catenulate sporulation, is shared in the Zoöpagaceae by the three genera *Acaulopage, Stylopage,* and *Cystopage.* On the other hand the endoparasitic genus *Cochlonema* and the ectoparasitic genus *Bdellospora* share its catenulate sporulation but differ markedly in outward form of the vegetative thallus. Of the seven species of *Zoöpage* that I have had occasion to describe earlier, six—*Z. atractospora* (**2**: 378–381), *Z. cladosperma* (**2**: 384–387), *Z. mitospora* (**4**: 137–140), *Z. nematospora* (**2**: 381–384), *Z. phanera* (**1**: 26–30), and *Z. thamnospira* (**4**: 141–144)—subsist by capture of *Amoebae,* whereas the seventh, *Z. tryphera* (**3**: 241–244), subsists by preying habitually on a testaceous rhizopod. Three fungi are set forth in the present paper as new members of the genus; two of them capturing *Amoebae,* whereas the third, a species remarkable especially for

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[MYCOLOGIA for May–June (**39**: 253–377) was issued June 19, 1947]

the hyphomycete-like appearance of its conidia, captures a testaceous rhizopod.

A NARROW-SPORED ZOÖPAGE CAPTURING TWO SPECIES OF AMOEBA

Several maizemeal-agar plate cultures which, after being permeated with mycelium of *Pythium ultimum* Trow, were further planted with small quantities of partly decayed leaves of *Phragmites communis* Trin. collected near Madison, Wisconsin, on November 20, 1945, revealed in eight days capture of numerous individual amoebae through adhesion to meagerly branched aseptate hyphae varying commonly from 1 to 1.8 μ in width. The captured animals measured 10 to 40 μ across when drawn into a somewhat rounded form. Their finely granular transparent protoplasm was surrounded by a thin, firm pellicle which frequently was in part minutely rippled and in part was disposed in a rather smoothly undulating contour about broadly protruding pseudopodia. All newly captured specimens contained a single subspherical or prolate ellipsoidal nucleus in which a relatively large mass of clear, highly transparent material surrounded a smaller quantity of slightly darker material. This darker material sometimes was present as a globose central body or endosome (FIG. 1, *A, a–d; B*), and at other times was divided among about twelve oblate ellipsoidal bodies that were distributed in scattered positions close under the nuclear membrane (FIG. 1, *A, e, f; C, a, b; D, a*). From their different nuclear organization the animals were obviously referable to two separate species of *Amoeba* which in their morphology corresponded very closely to the two species earlier reported as being habitually captured and consumed by my *Acaulopage ischnospora* (**10**). The correspondence, indeed, left no doubt that the same two species were concerned here as had been concerned in the cultures of *A. ischnospora* prepared with plant detritus originating from a locality more than 150 miles from Madison. Since predaceous attack, and, for that matter, also parasitic attack, on different rhizopods is not often observable among members of the Zoöpagaceae, utilization of the same two species of *Amoeba* by both *A. ischnospora* and the present fungus would seem to indicate exceptional similarity in the animals with respect to composi-

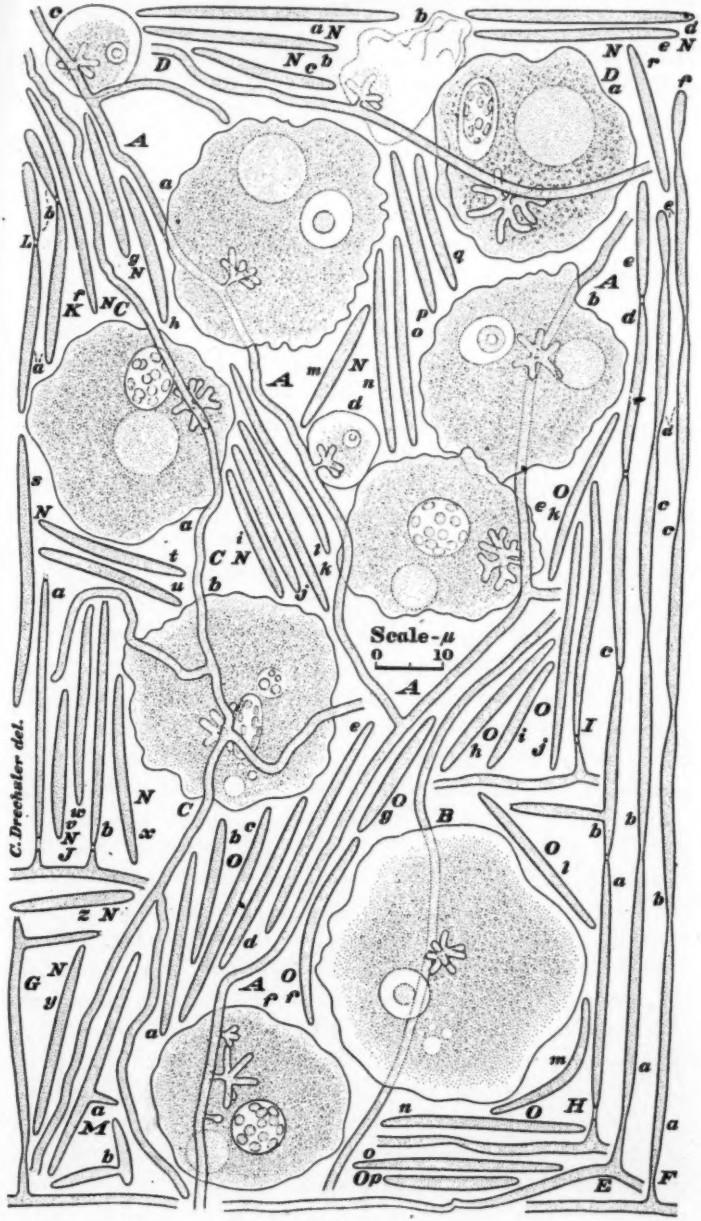

FIG. 1. *Zoöpage virgispora.*

tion of pellicle and protoplasm despite very evident differences in their nuclear organization.

Following capture of an indivdual amoeba its pellicle was penetrated by a narrow process extended from the adhering hyphal filament. After elongating a few microns this process would widen abruptly and bifurcate repeatedly to form a pedicellate haustorium, which like the similar organ in *Acaulopage ischnospora* bore short assimilative branches of about the same width as the mycelial hyphae. Usually only a single haustorium was formed (FIG. 1, *A, a–e; B; C, a, b; D, a, b*), but sometimes as many as three were intruded into an animal (FIG. 1, *A, f*) to expropriate its contents.

Expropriation of protoplasm was at the beginning not accompanied by any noticeable injury in specimens of the *Amoeba* whose nucleus contains the single central body, for the nucleus here retained its normal appearance and the contractile vacuole continued to operate briskly until the granular contents were reduced to perhaps one-third of their original quantity. Many individuals of the other *Amoeba,* however, showed at a relatively early stage of expropriation rather pronounced lengthening and narrowing of the nucleus, together with irregular deformation of the peripheral bodies (FIG. 1, *C, b; D, a*). It appears uncertain whether this deformation of the nucleus came about primarily as a result of invasion by the fungus, or perhaps was encouraged by the conditions—such as strong illumination and diminished air supply under a cover glass—usually attending close microscopical examination. Similarly early nuclear degeneration was not noted before when the same *Amoeba* was found subjected to predaceous attack by *Acaulopage ischnospora,* by *A. tetraceros* Drechsl. (**8**: 289–291), and by *Zoöpage thamnospira.* After captured animals of either species succumbed, expropriation of their contents continued (FIG. 1, *D, b*), until only the empty pellicle remained. Thereupon, as in related forms, the haustorium was evacuated through withdrawal of its contents backward into the parent hypha, leaving its empty membranous envelope to vanish like the pellicle surrounding it.

Thus amply nourished the fungus reproduced asexually in abundance by giving rise here and there from prostrate hyphae to erect or ascending aerial filaments, which, though for the most part of the same width as the mycelial threads, were constricted to about

one-third of this width at intervals varying usually from 15 to 40 μ (FIG. 1, *E, F*); the lowermost constriction coming usually at a height of 2 to 6 μ (FIG. 1, *E, F, G*). On cessation of growth the wider portions of the filaments (FIG. 1, *E, a–e; F, a–f*) were delimited as conidia through evacuation of each narrow isthmus, and deposition of a retaining wall at both ends of the emptied tubular connection (FIG. 1, *H, a–e; I; J, a, b; K, a, b; L, a, b*). The number of conidia formed in a uniaxial chain varied commonly from five to ten, but additional spores were often produced in a lateral chain attached to a spur extending at a wide angle from the lowermost conidium (FIG. 1, *G*), or from the conidium immediately above the lowermost one (FIG. 1, *H, b*). Apparently the lowermost conidium was often delimited proximally somewhat later than other members of the chain, since it was frequently found continuous with the mycelium (FIG. 1, *G*) when all of its fellows had already become detached. After its tardy delimitation from the tapering sterigma it yet appeared as a rule distinguishable from spores of more distal origin by reason of its greater length and lesser width—in fine, by reason of its more pronouncedly filamentous shape (FIG. 1, *H, a; I; J, a, b*). The terminal conidium (FIG. 1, *H, e; K, b; L, b*), on the other hand, was often noticeably shorter than the conidia formed below it (FIG. 1, *H, a–d; K, a; L, a*), besides being distinguished frequently by a more nearly clavate shape. Although occasionally the conidial chains were borne on sterigmata less than 10 μ apart (FIG. 1, *J, a, b*) the intervals between sterigmata were usually many times greater. Sporulation, nevertheless, was so abundant that after disintegration of the chains the detached conidia were strewn thickly over the substratum, and then offered a display reminiscent of the detached conidia of *Acaulopage ischnospora*, owing mainly to a general similarity of shape that presumably derives from like adaptation for predaceous attack on the same two rhizopods. On more careful examination the conidia of the catenulate fungus showed trustworthy distinguishing features in their occasionally branched condition (FIG. 1, *M, a, b*), their lesser length, and their lack of empty appendages (FIG. 1, *N, a–z; O, a–p*). The catenulate conidia further showed considerable similarity in outward form to the solitary conidia of my *A. stenospora* (**7**: 254, 256–258); and

this similarity, too, may derive from adaptation to a like biological relationship, since the *Amoeba* captured by that fungus has a nucleus with a central body, and therefore might be identical with one of the two rhizopods found destroyed in the cultures planted with decaying *Phragmites* leaves. No close resemblance in conidial morphology was discovered through comparison with previously described species of *Zoöpage,* for all these differ markedly either with respect to dimensions, or to shape, or to presence of warty sculpturing. The catenulate fungus from Wisconsin is accordingly described as a new species under an epithet having reference to the rod-like conformation of its conidia.

Zoöpage virgispora sp. nov.

Mycelium effusum; hyphis continuis, incoloratis, filiformibus, parce ramosis, plerumque 1–1.8 μ crassis, ad animalia minuta inhaerentibus, pelliculam eorum perforantibus, haustorium (interdum 2 vel 3 haustoria) intus evolventibus quod protoplasma exhaurit; haustorium pediculatum, pediculo 2–4 μ longo, 0.6–1 μ crasso, apice abrupte latescente, vulgo bis vel ter repetite bifurco, itaque saepius 4–8 ramulos assumentes divaricatos 2–6 μ longos 1.1–1.4 μ crassos ferente. Conidia continua, incolorata, levia, saepius baculiformia, utrimque leniter attenuata, interdum filiformia aut clavata, nonnunquam ramo praedita, 11–41 μ longa, 1.2–2.2 μ crassa, in catenulis oriunda; catenulis ex apice sterigmatis erecti 2–6 μ longi ascendentibus, saepius simplicibus sed interdum ramosis, vulgo in 5–10 sporis constantibus.

Amoebas duarum specierum 10–40 μ latas capiens consumensque habitat in foliis *Phragmitis communis* putrescentibus prope Madison, Wisconsin.

Mycelium spreading; vegetative hyphae continuous, colorless, filamentous, rather sparingly branched, mostly 1 to 1.8 μ wide, capturing minute animals through adhesion, then narrowly perforating the pellicle of each captive and intruding a haustorium (or sometimes 2 to 3 haustoria) to assimilate the protoplasmic contents. Haustorium pedicellate, the pedicel usually 2 to 4 μ long, 0.6 to 1 μ wide, abruptly enlarging distally and bifurcating 2 or 3 times at wide angles, thus bearing usually 4 to 8 assimilative branches 2 to 6 μ long and 1.1 to 1.4 μ broad. Conidia continuous, colorless, smooth, most often rod-shaped, tapering noticeably toward both ends, sometimes filamentous or clavate, sometimes bearing a branch at nearly a right angle, mostly 11 to 41 μ long, 1.2 to 2.2 μ wide, formed in chains; the chains mostly simple and containing 5 to 10 spores, but sometimes branched and then containing often 10 to 15 spores altogether, in either case ascending from an erect sterigma usually 2 to 6 μ long.

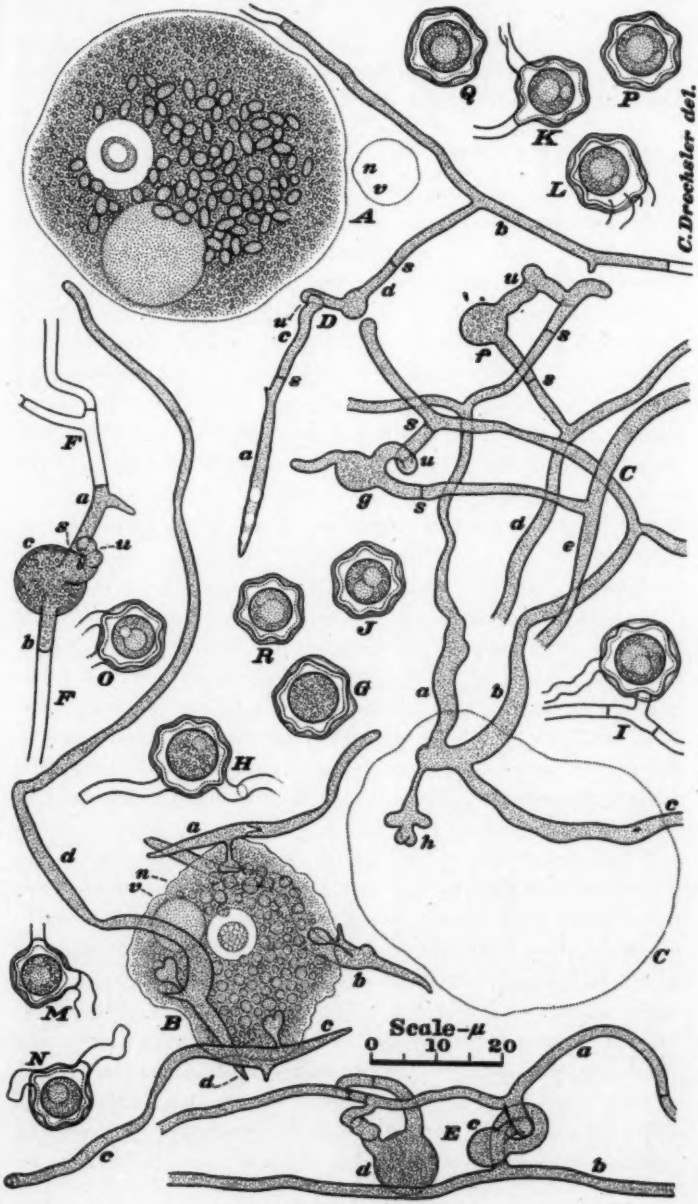

FIG. 2. *Zoöpage pachyblasta.*

Capturing and consuming *Amoebae* 10 to 40 μ wide that belong to two species, it occurs in decaying leaves of *Phragmites communis* near Madison, Wisconsin.

A ZOÖPAGE WITH CONIDIA THAT OFTEN HAVE WIDE GERM HYPHAE

A number of soft maizemeal-agar plate cultures which, after being permeated with mycelium of *Pythium ultimum* Trow, had been further planted by adding small quantities of partly decayed potato-vine (*Solanum tuberosum* L.) detritus collected near Greeley, Colorado, early in October, 1945, soon became abundantly inhabited by an *Amoeba*, mostly 25 to 50 μ wide, which when examined under a microscope of high magnification did not appear to be surrounded by a distinct pellicle. Should an outer membrane corresponding to a pellicle have been present it must have been too thin to be clearly discernible. The transparency of the animal's protoplasm was greatly reduced by numerous ingested bodies, which in some instances could readily be recognized as fungus spores (FIG. 2, *A*), but in other instances seemed of rather ambiguous character (FIG. 2, *B*; FIG. 3, *A*). Very often the opaque ingested material completely hid the single nucleus of the rhizopod. Where, however, pseudopodial movement had brought the nucleus into a favorable position on the upper side of the animal, it was revealed as a globose body, about 7 to 11 μ wide (FIG. 2, *A, n; B, n;* FIG. 3, *A, n*), consisting of a clear homogeneous outer layer and a subspherical central endosome; the endosome offering a somewhat darker appearance, except for a clear vacuole enclosed by it (FIG. 2, *A, n;* FIG. 3, *A, n*).

When the soft agar cultures were examined fourteen days after the potato-vine detritus had been added, numerous specimens of the *Amoeba* were found undergoing destruction by a species of *Zoöpage* whose branched conidial chains appeared more or less interlaced in nearly horizontal postures to form a scanty arachnoid aerial weft (FIG. 3, *B*). In following the branched chains backward they were found arising from aseptate filaments that came from scattered animals in various stages of disintegration (FIG. 3, *B, a–c*). While the aseptate filaments for the most part measured about 1.7 μ in width, they often showed distally one or more constrictions whereby hyphal portions (FIG. 3, *C, a; D, a*) were set

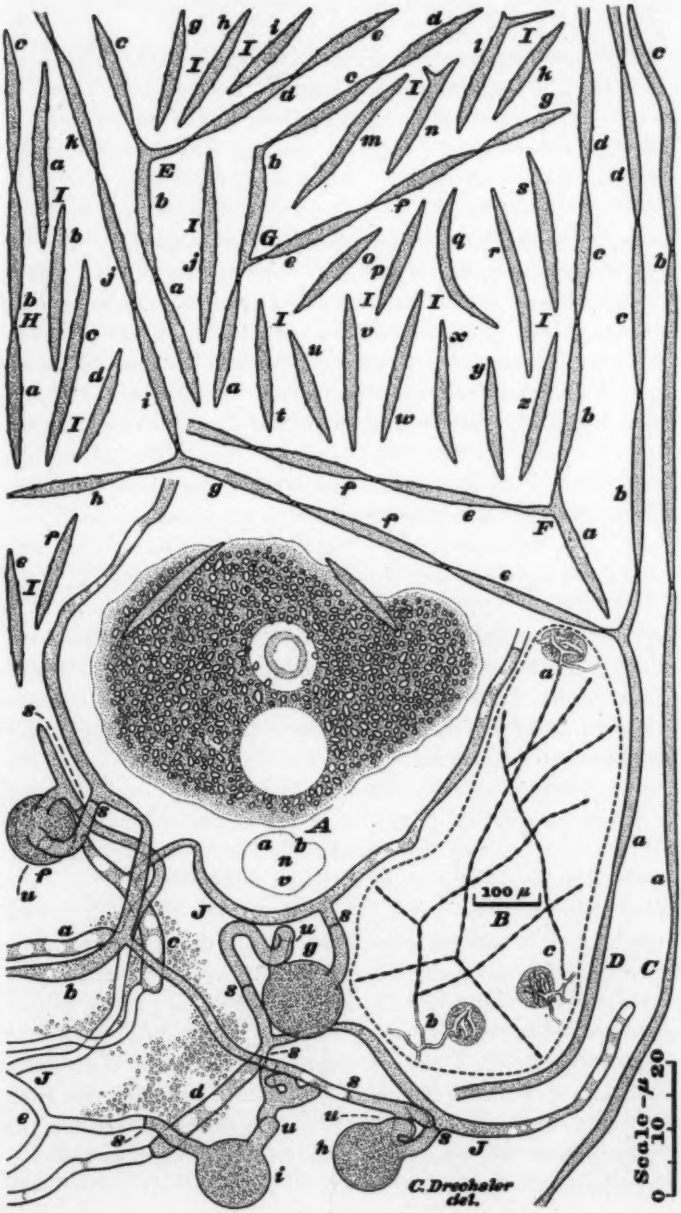

FIG. 3. *Zoöpaga pachyblasta.*

off, generally similar to the adjacent conidia (FIG. 3, *C, b, c*), as these likewise frequently attained lengths from 40 to 50 μ, and as a rule, even when measuring only about 25 μ (FIG. 3, *D, b–e*), were smooth externally. Above the few poorly differentiated proximal conidia all members of a conidial chain (FIG. 3, *D, f–k; E, a–e; F, a–f; G, a–g; H, a–c*) were found ornamented with many verrucose protuberances that appeared conspicuous when the spores were viewed in air bubbles. Since a chain often contained twenty to thirty-five members in a uniaxial series, and in addition frequently bore one or two branches, each of three to fifteen spores, it is not surprising that detached conidia in a random assortment (FIG. 3, *I, a–z*) showed usually so strong a preponderance of verrucose specimens that the few intermixed smooth specimens (FIG. 3, *I, r*) were hardly noticeable. Conidial chains usually bore their branches at wide angles; the branches arising from distal and medial positions in the axial series as well as from proximal positions. The lateral spur supporting a branch seemed to arise somewhat more often near the distal end of a conidium (FIG. 3, *D, g; E, b; F, a; I, l, n*) than near the basal end (FIG. 3, *G, b*). In tapering toward the narrow isthmuses between members of a chain, the conidia showed generally an elongate fusiform shape rather similar to the shape of the conidia of *Z. atractospora*. On disintegration of the chains the spores were left strewn about thickly on the moist substratum. When a roving specimen of the susceptible *Amoeba* species came in contact with them they adhered to the animal (FIG. 3, *A, a, b*). Such adhering spores commonly germinated by putting forth individually a germ-tube (FIG. 2, *B, a, b*) which near its origin soon attained a width—often 3.5 to 4 μ—about twice their own (FIG. 2, *B, c, d*), though in extending itself well beyond the animal, whether on or into the agar substratum, it conformed to the usual width of mycelial hyphae generally. At the same time that each adhering conidium was putting forth a germ-tube it was also intruding into the protoplasm of the animal a haustorium which in an early stage consisted usually of a slender stalk with a swollen termination (FIG. 2, *B, b*) or with two stout divergent lobes (FIG. 2, *B, a, c, d*). On further bifurcation the haustorium in later stages was often found bearing four assimilative lobes (FIG. 2, *C, h*).

Although the proximally widened germ-tube coming from an adhering conidium may properly be held distinctive of the fungus, the extraordinary width here is probably not a special attribute of germ-tubes, but rather a general attribute of adhering vegetative hyphae. As a rule when an attack was well advanced the *Amoeba* was found closely beset over a considerable portion of its surface with conspicuously widened hyphal ramifications (FIG. 2, *C*, *a–c*) that in many instances seemed to be of mycelial origin as they lacked the pointed spurs wherein the tapered ends of a conidium usually remained recognizable. The widening of hyphal elements may perhaps be best interpreted as an adaptational feature which, by providing increased adhesive surface, makes for greater effectiveness in holding rhizopods whose lack of a firm pellicle must make them unusually elusive. In instances where a detached conidium (FIG. 2, *D*, *a*) collaborated with a mycelial filament (FIG. 2, *D*, *b*) to give rise to a pair of conjugating gametangia (FIG. 2, *D*, *c*, *d*), the gametangium contributed by the conidium (FIG. 2, *D*, *c*) was borne on a germ-tube of ordinary width.

Units of sexual reproductive apparatus derived jointly from a conidium and a mycelial filament showed much the same relationship of parts as was displayed in similar units, for example, of *Stylopage ischnospora*. The gametangia became delimited basally by cross-walls (FIG. 2, *D*, *s*) at about the same time they were conjugating apically (FIG. 2, *D*, *u*); and soon thereafter the globose swelling in which the zygospore was to be formed began to develop in one of the gametangia—more usually in the one (FIG. 2, *D*, *d*) contributed from the mycelial hypha. Sexual reproductive apparatus contributed jointly from conidia and mycelial hyphae appeared, however, much less abundant than in *S. ischnospora;* most units here seeming to come from hyphae which either had not originated at all directly from a conidium, or, at least, were no longer recognizable as germ-tubes. In contrast to conidial chains, which usually ascended from promiscuously scattered positions, sexual apparatus was produced very largely in immediate proximity to a disintegrating animal. Prolongations or ramifications of the several widened hyphal elements (FIG. 2, *C*, *a–d;* FIG. 3, *J*, *a–e*) would put forth branches that soon became paired. After deposition of cross-walls in the branches (FIG. 2, *C*, *s;* FIG. 3, *J*, *s*)

and apical fusion (FIG. 2, *C, u;* FIG. 3, *J, u*) of the gametangia thus delimited, a globose swelling or zygosporangium (FIG. 2, *C, f, g;* FIG. 3, *J, f–i*) would begin to form in one of the conjugating cells, usually at a distance between 5 and 10 μ from the place of union. Most frequently the two gametangia in a pair would be contributed from separate adhesive hyphae; such diclinism being very common immediately around disintegrating animals where sexual branches were generally present in greater abundance than some distance away. Yet propinquity of two congenial hyphae did not always insure a diclinous origin of sexual apparatus; for in some instances a mycelial hypha (FIG. 2, *E, a*) was found collaborating with another (FIG. 2, *E, b*) to produce a diclinous zygosporangium (FIG. 2, *E, c*) while less than 25 μ away it was forming a monoclinous zygosporangium (FIG. 2, *E, d*). If in some monoclinous reproductive units the two gametangia were borne terminally on separate branches arising close together from the same parent hypha (FIG. 2, *E, d*), in other monoclinous units the gametangia were represented by adjacent hyphal segments (FIG. 2, *F, a, b*) separated by an ordinary cross-wall (FIG. 2, *F, s*). Where the latter arrangement of parts occurred, each of the adjacent segments would put forth a short arching outgrowth. The two outgrowths, on meeting one another, united apically (FIG. 2, *F, u*) to form a bail-like conjugation-tube somewhat similar to the conjugation-tube in my *Acaulopage gomphoclada* (**8**: 278–283), but apparently never winding about the axial hypha. Following conjugation one of the gametangia would swell out locally into a globose excrescence (FIG. 2, *F, c*) that after attaining definitive size through accession of protoplasmic material contributed from both gametangia gave rise to a zygospore in much the same way as zygosporangia of more usual origin. In all sexual reproductive units alike the globose zygosporangial envelope later was found collapsed loosely about the boldly undulating zygospore wall, which, as in my *Acaulopage marantica* (**5**: 143–149), had the appearance of being separated from the spherical protoplast contained within it (FIG. 2, *G–R*). This protoplast at first seemed to be of uniformly granular texture (FIG. 2, *G, H*), though later it showed often two (FIG. 2, *I, J*) or three homogeneous reserve globules, and at full maturity it appeared to have the internal organization

most usual in oöspores—the granular material being collected in a peripheral layer surrounding a single reserve globule and a smaller refringent body (FIG. 2, *K–R*).

The fungus is described under a specific name having reference to the frequently extraordinary width of the germ-tubes produced by its conidia.

Zoöpage pachyblasta sp. nov.

Mycelium effusum; hyphis filiformibus, incoloratis, primum continuis, parce ramosis, plerumque 1–2.4 μ (vulgo circa 1.7 μ) crassis, ad animalia minuta inhaerentibus, tum in partibus haerentibus saepius usque 4 μ latescentibus et ibi haustoria intus evolventibus quae protoplasma exhauriunt; haustorio ex pediculo 1–4 μ longo, 0.5–1 μ crasso et 2–4 ramulis assumentibus divaricatis 2.5–9 μ longis, 2–3 μ latis constante. Conidia incolorata, plerumque simplicia, interdum furcata, in catenulas ascendentes longas simplices vel ramosas digesta, prope basim catenulae saepius filiformia, levia, 30–50 μ longa, circa 1.7 μ crassa, in apice catenulae interdum clavata, in partibus catenulae intermediis plerumque elongato-fusiformia, utrimque acutula, distincte verrucosa, plerumque 15–30 μ longa, 1.6–2.3 μ crassa; hypha germinationis saepe circa 1.5 μ crassa, sed ubicumque in animali adhaerente vulgo 3–4 μ crassa. Gametangia plerumque 10–25 μ longa, ambo interdum ex cellulis unae hyphae intercalaribus contiguis constantia denique tubulo curvato conjungentia, sed saepius ambo in cellulis terminalibus constantia, nunc in duabus ramulis unae hyphae nunc in duabus ramulis aliarum hypharum oriunda, nunc alterum in tubo germinationis alterum in ramulo mycelii ortum, quandocumque terminalia apice conjungentia. Zygosporangium circa 5 μ sub junctura oriundum, plerumque 9–12.5 μ in diametro, primo leve, in maturitate membrana circum zygosporam laxe collapsa; zygospora flavida, globosa, valde verrucosa, 8.5–12 μ in diametro, membrana undulata ejus cellulam viventem sphaeralem 5.7–8 μ crassam laxe circumdante.

Amoebas 25–50 μ latas capiens consumensque habitat in foliis caulibusque *Solani tuberosi* putrescentibus prope Greeley, Colorado.

Mycelium spreading; vegetative hyphae filamentous, colorless, sparingly branched, at first continuous, mostly 1 to 2.4 μ (average about 1.7 μ) wide, adhering to minute animals, in the adhering portions often widening to 4 μ and from these portions intruding haustoria to appropriate the protoplasmic contents; haustorium consisting of a pedicel, 1 to 4 μ long and 0.5 to 1 μ wide, together with 2 to 4 assimilative branches 2.5 to 9 μ long and 2 to 3 μ wide. Conidia colorless, mostly simple, sometimes branched, arranged in long, simple or branched, ascending chains—those at the base of a chain often filamentous, smooth, 30 to 50 μ long, and about 1.7 μ wide, the one at the end of a chain sometimes clavate, those in intermediate portions of a chain mostly elongate fusiform, somewhat pointed at both ends, distinctly verrucose, mostly 15 to 30 μ

long and 1.6 to 2.3 μ wide; the germ hypha often about 1.5 μ wide, but on the adhering animal commonly enlarging to a width of 3 to 4 μ. Gametangia mostly 10 to 25 μ long, both of a pair sometimes consisting of contiguous intercalary hyphal segments, and then conjugating through production of curved branches and through the union of these branches into an arcuate lateral connection; but both gametangia more often consisting of terminal hyphal segments borne on branches arising either from the same hypha or from different hyphae, and then, as also when occasionally one is supplied from a mycelial hypha while the other is supplied from a germinating conidium, conjugating apically. Zygosporangium usually formed about 5 μ from place of union, commonly 9 to 12.5 μ in diameter, at first smooth, its envelope at maturity collapsing loosely about the zygospore; zygospore yellowish, subspherical, boldly verrucose, 8.5 to 12 μ in diameter, its undulating wall at maturity loosely enveloping a globose living protoplast 5.7 to 8 μ in diameter.

Capturing and consuming an *Amoeba* usually 25 to 50 μ wide it occurs in decaying leaves and stems of *Solanum tuberosum* near Greeley, Colorado.

A DENDRYPHIUM-LIKE ZOÖPAGE THAT PREYS ON A TESTACEOUS RHIZOPOD

Several maizemeal-agar plate cultures which after being permeated with mycelium of *Pythium ultimum* Trow had been further planted with small quantities of partly decayed barley (*Hordeum vulgare* L.) straw gathered near Greeley, Colorado, early in October, 1945, showed after sixteen days in areas bordering the superadded material some sparse development of a catenulate fungus that in its gross appearance recalled the hyphomycetous genera *Dendryphium* and *Helminthosporium*. The same catenulate fungus subsequently came to light also in a culture of *P. ultimum* to which had been added a few pinches of friable detritus from partly decayed potato vines likewise collected near Greeley, Colorado, in October, 1945. Its sparse mycelium in all instances consisted of hyphae about 1.7 μ wide that gave off branches here and there, each of which entered the aperture of a testaceous rhizopod to terminate near the fundus of the animal in a simple and often somewhat irregular coil (FIG. 4, *A, a, b; B, a, b; C, a–c.* FIG. 5, *A–D; E, a–d*). Specimens of the rhizopod thus invaded were of somewhat compressed ovoid shape. Their testae, composed of

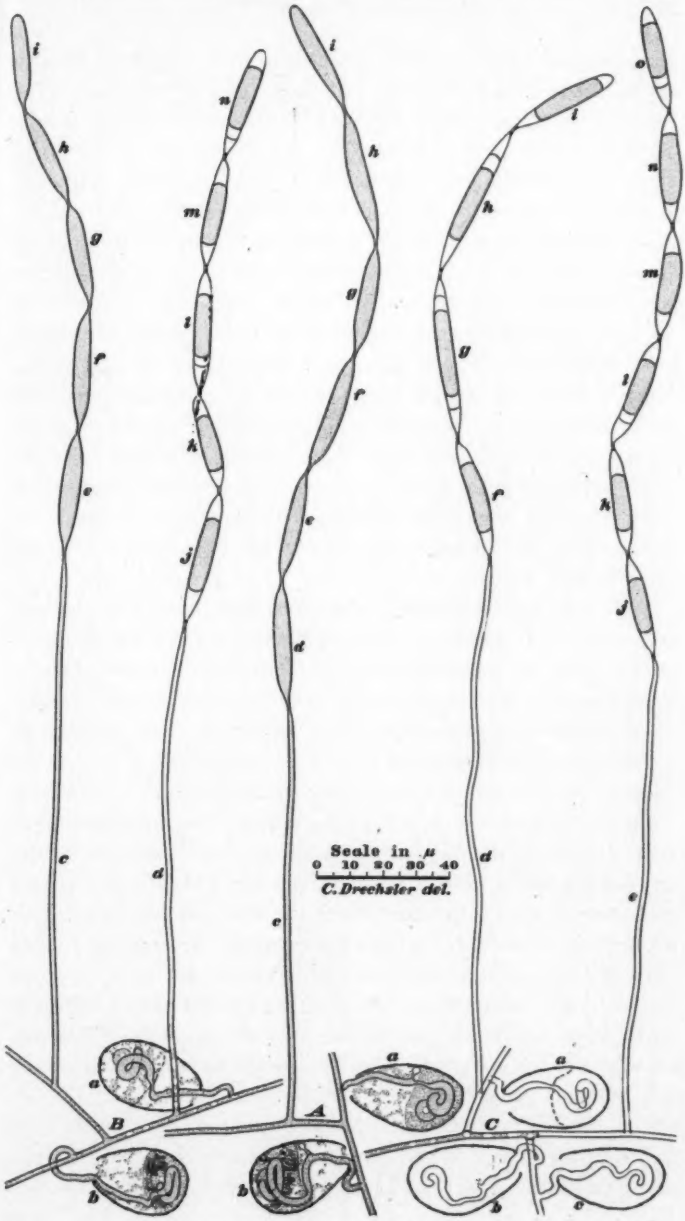

FIG. 4. *Zoöpage toechospora.*

obscurely imbricated scales, measured commonly 28 to 38 μ in length, 19 to 21 μ in breadth, and about 15 μ in thickness. The aperture usually measured about 7 μ in width. The single spherical nucleus (FIG. 4, *A, a, b; B, a, b.* FIG. 5, *A–C*) varied in diameter from 6.2 to 8.2 μ, and contained a globose endosome 2 to 2.8 μ in diameter. In many invaded animals the relatively thick outer layer of nucleoplasm showed a slightly alveolar or faintly granular structure (FIG. 5, *A–C*), and thereby offered an appreciably darker appearance than the endosome. It seems possible that in these instances the nucleus may have been revealing harmful modifications induced by the presence of the fungus. The morphological features shown by animals in normal condition corresponded well to those ascribed to *Euglypha laevis* (Ehrenb.) Perty in the taxonomic treatises of Penard (**11**: 512–513) and of Wailes (**12**: 32–34). The protozoan species here concerned seemed identical, at all events, with the species that under the binomial *E. laevis* was earlier set forth as being parasitized by my *Cochlonema pumilum* (**6**: 398–402; **9**: 9–14).

Since the invaded animals were found distributed over the surface of the agar cultures not in a haphazard manner but in recognizably linear arrangement along the rather straightforward mycelial filaments, it was evident that they had been arrested in their locomotion because of encounter with the fungus. Yet the locomotion of the animals could not have been halted immediately at the moment of encounter, for sometimes the aperture of a captive was found as much as 25 or 35 μ from the origin of the invading branch (FIG. 5, *E, b, d*)—a distance seemingly greater than the length of any pseudopodium broad enough to offer much likelihood of secure adhesion. Even in instances where the rhizopod was found with its aperture close to a long mycelial filament, the invading branch often pursued an irregular roundabout course for 10 to 20 μ before entering the aperture. In profile view the branch entering the aperture was often seen passing over the thickened projecting tip of one of the marginal scales, or between the projecting tips of two adjacent marginal scales (FIG. 4, *A, a, b; B, a, b; C, a–c.* FIG. 5, *A; C; D; E, a, c, d*), in either case making intimate contact with the testa. Where the positional relationships were not shown in profile view (FIG. 5, *B; E, b*) it often seemed fairly cer-

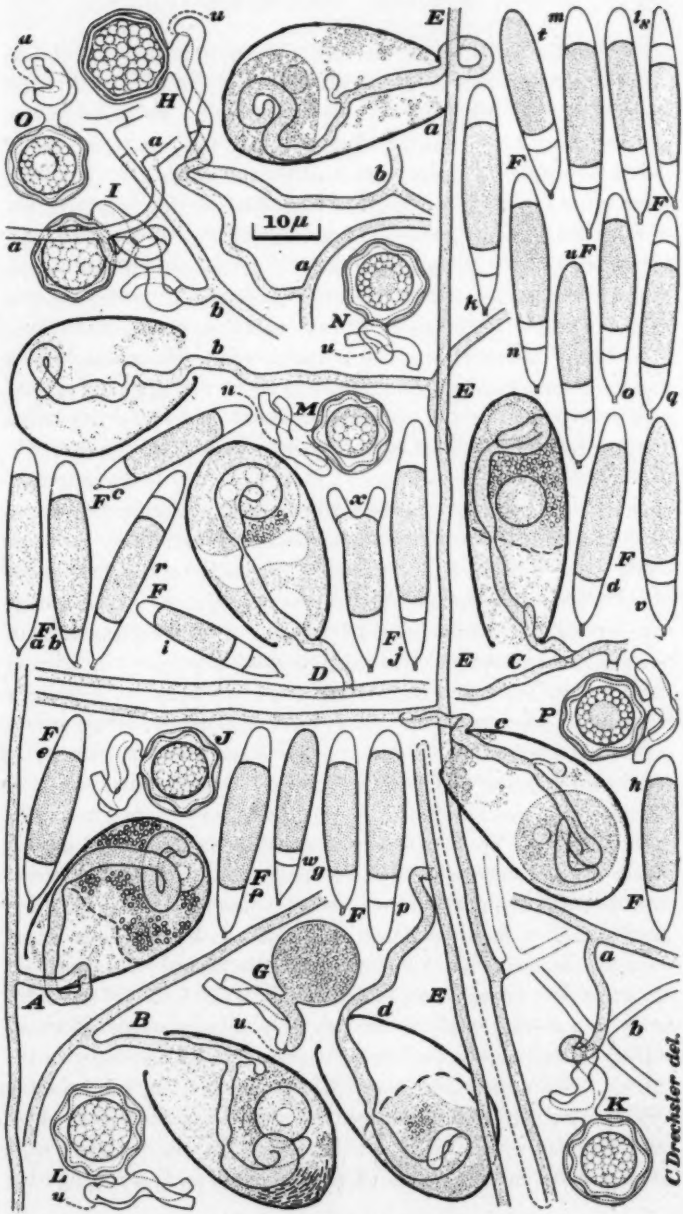

FIG. 5. *Zoöpage toechospora*.

tain, nevertheless, that the invading branch touched one or two of the marginal scales oriented flatwise to the observer. Although the invading branch may have been put forth promptly when a pseudopodium of the moving animal touched the mycelial filament, locomotion may not have halted—that is, capture may not have been effected—until the branch had reached the aperture and through adhesion had fastened upon one or two of the projecting serrulated scales. If, as seems likely, capture was effected mainly through adhesion to the testa rather than to the protoplast, the animal in many instances could reasonably be presumed to have moved some distance away before the tip of the elongating branch found a suitable holdfast; the growth made by the fungus in pursuit of the slow fugitive thus probably accounting for the frequently considerable length of the hyphal part to which the captive eventually came to be tethered.

In its course through the forward portion of the animal's interior the invading branch sometimes maintained approximately the same width (FIG. 5, *B; C; E, b*) it showed externally, although at other times it widened noticeably (FIG. 5, *A; D; E, a, d*). About midway toward the fundus it nearly always revealed a rather pronounced constriction which evidently marked the place where it had made its way through a barrier laid down by the animal seemingly in an attempt to prevent the fungus from reaching the deeper protoplasm and the nucleus. Often the barrier consisted principally of small platelets, that manifestly represented scales in early stages of development (FIG. 5, *A; C; E, d*); the siliceous parts normally destined to make up the testa of a new individual being used prematurely in an unsuccessful effort to protect the prospective parent from destruction. Yet in some instances where the animal contained unmistakably a supply of small scales (FIG. 5, *B*) it did not divert them to a defensive use, but, instead, like the animals that contained no scales in process of formation (FIG. 5, *D; E, a–c*), formed a much less distinctly visible barrier from a transparent substance similar to the substance normally composing cyst envelopes in the species. Some little distance above the constriction the invading hyphal branch frequently showed a rather abrupt bend, which in many instances was further distinguished by the presence of a small, saccate, narrowly attached appendage (FIG. 5, *B; E, a*)—the

curious arrangement thus presented probably having originated in an earlier and unsuccessful attempt at penetrating the animal's barrier. Beyond the constriction at the barrier the invading branch was prolonged often at the greatest width—from 3 to 4 μ—it attained anywhere (FIG. 5, *A; B; D; E, d*), though often, again, its width here—from 2 to 3 μ—did not markedly exceed its width in the anterior portion of the animal (FIG. 5, *C; E, a–c*). The terminal portion of the branch, as has been mentioned, was consistently coiled in noticeable measure, generally describing a single spiral or helicoid turn either in close proximity to the animal's nucleus (FIG. 5, *A, B*) or, less often, some distance away (FIG. 5, *C*). The terminally coiled hyphal branch, exclusive naturally of the part outside the testa, functioned as a haustorium in gradually depleting the animal of all protoplasmic materials (FIG. 5, *D; E, a–d*) until nothing remained but the empty shell; whereupon its own contents were withdrawn into the parent hypha (FIG. 4, *C, a–c*). While in its terminal coiling it offered some resemblance to the more elaborate assimilative apparatus of *Zoöpage thamnospira*, its virtually unbranched condition—the saccate appendage sometimes present and an occasional spur given off near the animal's mouth (FIG. 5, *C*) provided only a very meager display of ramification—makes the invading hyphal element conspicuous among haustoria of the Zoöpagaceae for simplicity of design. Indeed, with respect to simplicity it is probably surpassed in the family only by the outwardly undifferentiated assimilative branch of my *Acaulopage crobylospora* (**10**).

Thus amply nourished through the destruction of numerous captives the fungus reproduced asexually in some abundance. Prostrate mycelial hyphae gave rise here and there to erect filamentous branches (FIG. 4, *A, c; B, c, d; C, d, e.* FIG. 6, *A, a; B, a*) about 1.7 μ wide, which after attaining a height of 100 to 225 μ modified their further elongation through pronounced and rather evenly spaced fluctuations in width, thereby bringing into being a series of elongated ellipsoidal distended parts (FIG. 4, *A, d–i; B, e–i.* FIG. 6, *A, b–e; B, b–e*) connected by narrow isthmuses. When newly formed the distended parts, which commonly varied in number from four to six, usually measured from 25 to 40 μ in length and from 4.8 to 6 μ in width, whereas the isthmuses measured from 2 to

4 μ in length and 0.8 to 1 μ in width. From a consideration of conidial dimensions it seems probable that here as in most other catenulate Zoöpagaceae the distended parts subsequently increased appreciably in size through continued accession of protoplasmic material from the mycelium below. Although the chain of distended parts was usually found somewhat crooked rather than straight, it appeared remarkable that the very narrow isthmuses could sustain their massive burden so nearly in an erect posture. Since the hyphal membrane evidently maintained about the same thickness at the isthmuses as at the distended parts, the lumina of the isthmuses by way of which all distended parts were supplied—the lowermost one provided no exception since the tip of the supporting stalk was always markedly narrowed—hardly exceeded 0.5 μ or 0.6 μ in width. Because of difficulties of observation accompanying a dimension so minute, it was not clearly ascertained whether separation of the distended parts into individual conidia was accomplished by formation of cross-walls in the isthmuses, or by deposition of small quantities of plugging material in the narrow lumina, or by mere disintegration of the protoplasm within the isthmuses, or perchance by withdrawal of protoplasm from the isthmuses, followed possibly by slight collapse of the empty tubular membrane. In the disjunction of a conidial chain the isthmuses usually separated near the middle, so that each moiety eventually protruded from the end of a detached conidium as a rather well demarcated hilum.

During the maturation preceding such disjunction the supporting conidiophore was emptied of contents (FIG. 4, *B, d; C, d, e.* FIG. 6, *C, a; D, a; E, a, b*) and, further, each conidium was in large part evacuated as its entire protoplasmic contents were gathered into a segment embracing about three-fifths of the original volume of the spore (FIG. 4, *B, j–n; C, f–o.* FIG. 6, *C, b; D, b*). Among detached conidia representing terminal members of chains, many showed the living segment interposed between an empty locule at the hilum-bearing proximal end and an empty locule at the smoothly rounded distal end (FIG. 5, *F, a–h*). Almost equally numerous were specimens showing two empty cells at the basal end and one at the distal end (FIG. 5, *F, i–p.* FIG. 6, *F*), whereas the reversed arrangement with one empty cell at the proximal end and two empty cells

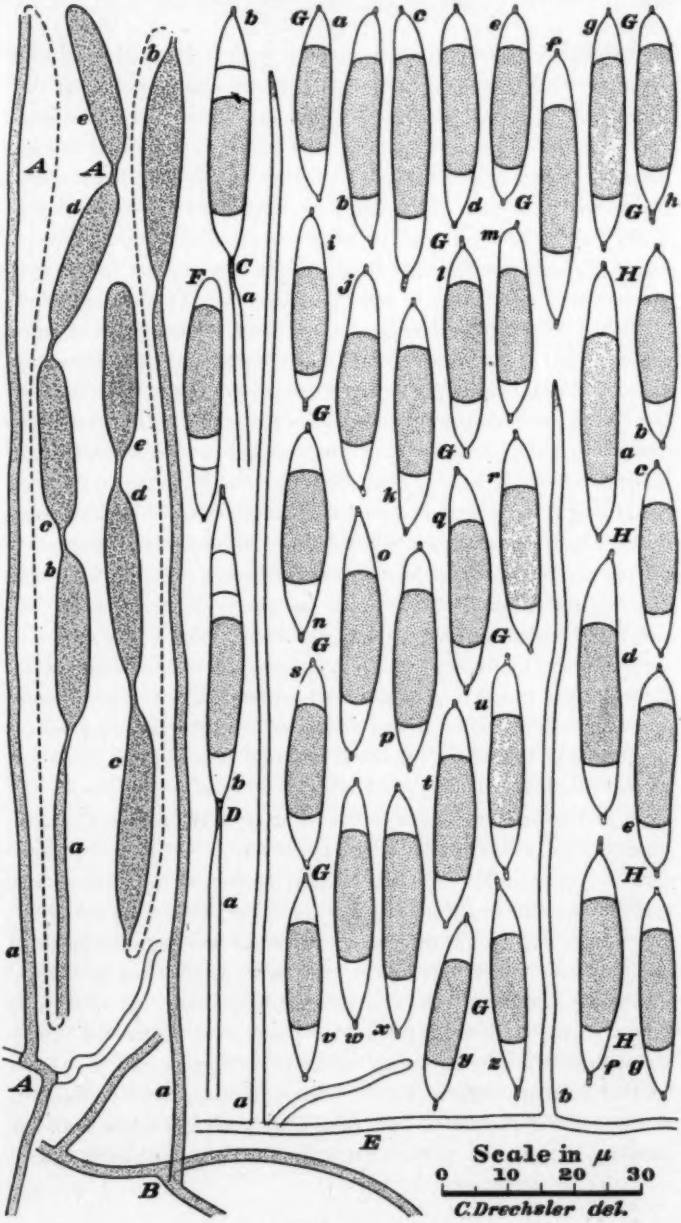

FIG. 6. *Zoöpage toechospora.*

at the distal end (FIG. 5, *F, q–s*) came under observation less frequently. Occasionally a terminal conidium was found filled with protoplasm clear to its rounded tip though furnished at the basal end with two empty locules (FIG. *F, t–w*); and somewhat rarely a bifurcate specimen of terminal origin bore an empty cell at the basal end as well as in each of the divergent arms (FIG. 5, *F, x*). A generally similar though slightly more varied distribution of empty locules prevailed among detached conidia that because of their development in intercalary or basal positions bore a protruding hilum at both ends, and therefore gave no reliable indication as to which of the ends was the proximal and which the distal one. Here likewise specimens with an empty cell at each end (FIG. 6, *G, a–z; H, a–g*) were most abundant, but almost equally numerous were specimens with a single empty cell at one end and two empty cells at the other end (FIG. 7, *A, a–z; B*). Some conidia of proximal or intercalary origin were furnished with four empty cells. The living segment in such spores appeared somewhat less often placed symmetrically between two empty segments at each end (FIG. 7, *C, a–c*) than disposed unsymmetrically between one empty segment at one end and three empty segments at the other end (FIG. 7, *D, a–f*). In some observed instances where the basal conidium remained attached to the supporting hypha after a cover-glass had been placed on the agar substratum, it was clearly evident that the spore bore a single empty cell at its proximal end and two (FIG. 6, *C, b*) or three (FIG. 6, *D, b*) empty cells at its distal end.

On and below the surface of the substratum the fungus gave rise sparingly to sexual reproductive apparatus of distinctive appearance (FIG. 5, *G–P*). In initiating development of a zygospore two zygophoric branches from separate mycelial filaments (FIG. 5, *H, a, b; I, a, b; K, a, b*) would become paired by winding distally about one another. In each branch a cross-wall would then be formed to delimit a terminal cell, or gametangium, usually 12 to 20 μ in length. Conjugation thereupon took place, in some instances being accomplished by the tip-to-tip fusion (FIG. 5, *L, u; N, u; O, u*) familiar in many related forms. Since, however, more often the rounded tips of the sexual cells were plainly not in contact with one another, conjugation perforce usually took place through lateral

fusion. While the place of union in many instances of lateral conjugation could not be distinctly made out, it seemed sufficiently clear in other instances that communication between the laterally apposed cells was sometimes established immediately below the two tips (FIG. 5, *G, u*) and sometimes fully 5 μ backward (FIG. 5, *M*). From a position commonly 2 to 8 μ below its apex, one of the gametangia would then put forth a globose excrescence that enlarged as it received protoplasmic material from the sexual branches. Usually the globose body reached a diameter of 12 to 15 μ before the gametangia became empty. As a separate zygospore wall made its appearance within the subspherical envelope, the protoplast underwent change from a granular (FIG. 5, *G*) to a globuliferous (FIG. 5, *H*) consistency. Thereupon the zygospore wall, which at first presented a somewhat angular outline, assumed a rather boldly undulating contour while the protoplast began to contract into a spherical form (FIG. 5, *I–L*). On further maturation a rather large homogeneous globule usually made its appearance in the center of the protoplast. Although in some instances the peripheral layer ultimately came to consist largely of granular material (FIG. 5, *M*), most zygospores appeared to retain during their resting period a pronouncedly globuliferous consistency in their peripheral protoplasmic layer (FIG. 5, *N–P*).

In the height of the erect hyphal branches supporting its conidial chains, as well as in the relatively great width and size of its conidia, the fungus departs markedly from the morphological trend expressed in other species of *Zoöpage*, and would seem to reveal close kinship rather with the genus *Stylopage*. While obviously the plural septa contained in the conidium are formed as retaining walls to mark a final stage, and often also one or two intermediate stages in the evacuation of the proximal and distal ends, the elongate ellipsoidal shape of the spore, together with the number and position of its partitions, makes for a remarkable resemblance to various species of *Helminthosporium*. The multiple septation of the conidium, so unusual for a catenulate member of the Zoöpagaceae, and, indeed, so strongly divergent from the spore morphology prevalent in the Phycomycetes, suggests for the fungus a specific epithet compounded partly of a word meaning "wall."

Zoöpage toechospora sp. nov.

Mycelium effusum; hyphis filiformibus, incoloratis, primum continuis, parce ramosis, plerumque 1.2–2 μ crassis, ad animalia minuta inhaerentibus, ea impedientibus, in quodque captivum unicum ramum intrudentibus qui protoplasma exhaurit; ramo in totum 40–80 μ longo, parte extra animal (retinaculo) 3–35 μ longa, 1.2–2 μ crassa, parte interna assumenti (haustorio) 30–50 μ longa, 2–4 μ lata, in medio animalis saepe flecta et interdum appendice sacculiformi praedita et praeterhac nonnunquam plus minusve constricta, deinde propius fundum animalis in spiram semel convoluta. Hyphae conidiophorae incoloratae, erectae, plerumque 100–225 μ altae, 1.5–1.8 μ crassae, apice usque 1 μ attenuatae, ibi 4–6 conidia copulis 2–4 μ longis, 0.8–1 μ crassis in catenulam connexa ferentes; conidiis incoloratis, elongato-ellipsoideis vel aliquid fusiformibus, quandocunque in summa catenula oriundis sursum rotundatis et rarenter bifurcis sed quandocunque alibi ortis semper simplicibus et post disjunctionem utrimque in copulam ruptam acutule abeuntibus, plerumque rectis sed interdum parum curvatis, 24–54 μ longis, 4.4–7 μ latis, in unica cellula viventi 15–26 μ longa et 2–4 (plerumque 2 vel 3) cellulis vacuis 2–10 μ longis consistentibus, ita utroque extremo saepissime 1 vel 2 cellulis vacuis praeditis, rarenter uno extremo aut protoplasmatis repletis aut 3 cellulis vacuis praeditis. Rami zygosporiferi saepe 15–55 μ longi, ambo ex aliis hyphis mycelii oriundi, inter se vulgo aliquantulum circumplicantes, primum continui, postea uterque septo cellulam sexualem (gametangium) terminalem 12–20 μ longam, 1.5–3 μ crassam delimitans; ambabus cellulis prope apicem vel usque 5 μ sub apice conjunctis utravis 2–8 μ sub apice zygosporangium gignente; zygosporangio sphaerali, plerumque 12–15 μ in diametro, primum levi, in maturitate membrana ejus circum zygosporam laxe collapsa; zygospora paululum flavida, globosa, 11–13.5 μ in diametro, valde verrucosa, membrana undulata ejus cellulam viventem laxe circumdante; cellula viventi sphaerali, 8–9.5 μ crassa, multis globulis farcta.

Euglypham laevem capiens consumensque habitat in stramento (foliis acere caulibusque) *Hordei vulgaris* putrescenti et foliis caulibusque *Solani tuberosi* putrescentibus prope Greeley, Colorado.

Mycelium spreading; vegetative hyphae colorless, filamentous, sparingly branched, at first aseptate, mostly 1.2 to 2 μ wide, capturing minute animals through adhesion, then sending a branch into each captive to assimilate its protoplasmic contents; the invading branch often 40 to 80 μ in total length, consisting of a proximal external portion (tether) 3 to 35 μ long, together with a distal assimilative portion (haustorium), 30 to 50 μ long and 2 to 4 μ wide, which often is bent markedly near the middle of the animal where it sometimes bears a sac-like appendage besides being modified by a pronounced constriction, and which terminates beyond the constriction in a spiral coil of approximately one turn. Conidiophorous hyphae colorless, erect, mostly 100 to 225 μ high, 1.5 to 1.8 μ wide, narrowing to a width of about 1 μ at the apex whereon is borne a chain of 4 to 6 conidia held together by connections 2 to 4 μ long

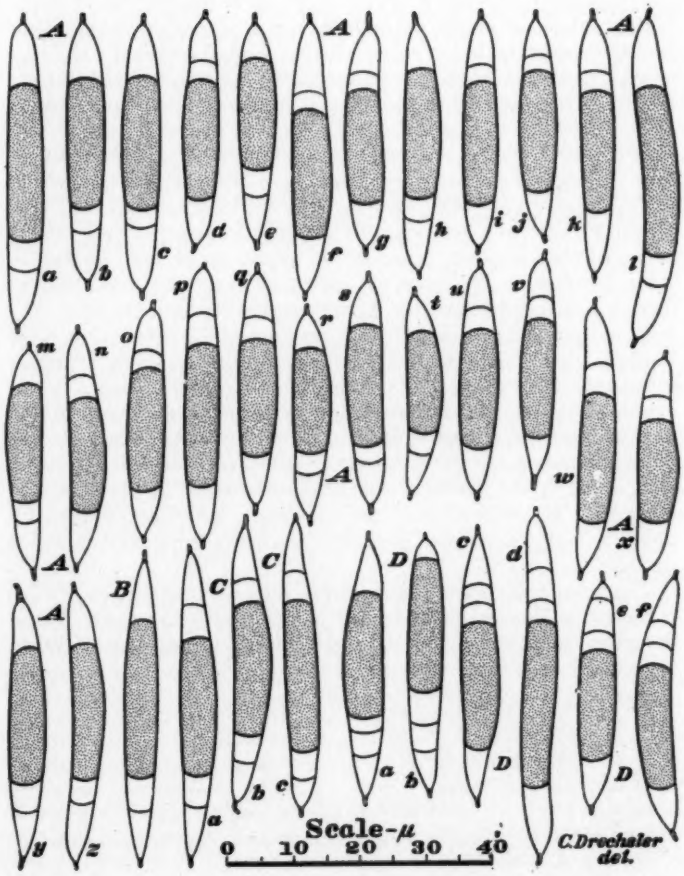

FIG. 7.

and 0.8 to 1 μ wide; conidia colorless, elongated ellipsoidal or somewhat spindle-shaped, always rounded at the tip when formed at the end of a chain and then occasionally forked, but when formed elsewhere in a chain always unbranched and after disarticulation terminating somewhat sharply at both ends in a projecting stump of the broken connection, in any case (whether formed terminally or lower down) mostly straight though sometimes slightly curved, mostly 24 to 54 μ long and 4.4 to 7 μ wide, consisting of one living segment 15 to 26 μ long, together with 2 to 4 (mostly 2 or 3) empty segments 2 to 10 μ long, and thus usually provided at each end with 1 or 2 empty segments, rarely being provided at one end with 3 empty segments or filled clear to one end with protoplasm. Zygophoric branches often 15 to 55 μ long, the two of a pair arising from separate hyphae, commonly winding about one another in some measure, at first aseptate, each later forming a cross-wall to delimit a terminal sexual cell (gametangium) commonly 12 to 20 μ long and 1.5 to 3 μ wide; after conjugation of the sexual cells at or immediately below their apices or backward from their apices as much as 5 μ, one of them giving rise 2 to 8 μ from its tip to a lateral zygosporangium; the zygosporangium subspherical, mostly 12 to 15 μ in diameter, at first smooth but at maturity its membrane collapsing loosely about the zygospore; zygospore somewhat yellowish, globose, 11 to 13.5 μ in diameter, boldly verrucose, its pronouncedly undulating membrane loosely surrounding a spherical living protoplast, 8 to 9.5 μ in diameter, which usually contains numerous globules.

Capturing and consuming *Euglypha laevis* it occurs in partly decayed straw (leaves, chaff, and stems) of *Hordeum vulgare* and in decaying leaves and stems of *Solanum tuberosum* near Greeley, Colorado.

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EXPLANATION OF FIGURES

FIG. 1. *Zoöpage virgispora;* drawn to a uniform magnification with the aid of a camera lucida; × 1000. *A,* Portion of mycelium with six captured amoebae; four of the animals, *a–d,* belong to a species distinguished by a nucleus with a single central body, whereas the two others, *e–f,* belong to a species having a nucleus with about twelve flattened ellipsoidal peripheral bodies. *B,* Portion of hypha with a captured specimen of the *Amoeba* whose nucleus contains a single central body. *C,* Portion of mycelium with two captured individuals, *a* and *b,* of the *Amoeba* whose nucleus contains about twelve peripheral bodies; the nucleus of one animal, *a,* appears normal, whereas that in the other, *b,* is abnormally elongated. *D,* Portion of hypha with two captured amoebae, *a* and *b;* one of the animals, *a,* shows an abnormally elongated nucleus in which about twelve somewhat degenerate peripheral bodies are visible; the other, *b,* represented by an almost completely empty pellicle, cannot be identified owing to disappearance of its nucleus. *E,* Portion of prostrate mycelial filament bearing a fertile hypha wherein five parts, *a–e,* destined for conversion into conidia, are shown connected by narrow isthmuses. *F,* Portion of prostrate mycelial filament bearing a fertile hypha wherein six expanded parts, *a–f,* destined for conversion into conidia, are shown connected by narrow isthmuses. *G,* Portion of mycelial filament shown still continuous with the branched basal member of a chain; all other members of the axial chain, as well as all members of the branch attached to the spur, have become detached. *H,* Portion of prostrate hypha with a sterigma whereon is attached a chain of five conidia, *a–e. J,* Portion of prostrate hypha with two sterigmata unusually close together; on them are shown attached two conidia, *a* and *b,* representing basal members of spore chains. *K, L,* Distal portions of two conidial chains, showing in each a subterminal conidium of ordinary length, *a,* and a relatively short terminal conidium, *b,* of somewhat clavate shape. *M,* Detached conidia, *a* and *b,* each with a lateral spur whereon was borne earlier a lateral branch of a conidial chain. *N* (*a–z*), *O* (*a–p*), Detached conidia, showing usual variations in size and shape.

FIG. 2. *Zoöpage pachyblasta;* drawn to a uniform magnification with the aid of a camera lucida; × 1000. *A,* Well-developed, normal specimen of *Amoeba* sp. habitually captured by the fungus; besides its nucleus, *n,* and its contractile vacuole, *v,* the animal contains numerous spores of an unidentified fungus. *B,* Specimen of *Amoeba* sp. into whose protoplasm four adhering conidia, *a–d,* have each intruded a haustorium in early stage of development; each conidium has also put forth a germ hypha; the germ hyphae extended from *c* and *d* have widened markedly in their proximal portions which are in contact with the animal; *n,* nucleus of animal, showing alveolar markings in the central body; *v,* contractile vacuole. *C,* Specimen of *Amoeba* sp. held captive through adhesion to several ramifying hyphae; only one ramifying system, which includes three adhering branches, *a–c,* is shown in contact with the animal, though two other ramifying systems are represented in the distal hyphal parts *d* and *e;* gametangia contributed from *a* and *b* have conjugated with gametangia from *d* and *e,* respectively, leading to development of the zygosporangia *f* and *g,* respectively; *s,* septa delimiting gametangia; *u,* place of union between gametangia. *D,* Unit of sexual reproductive apparatus contributed from a germinating conidium, *a,* and a mycelial filament, *b;* the former supplying the gametangium *c,* the latter the gametangium *d;* after apical conjugation of the gametangia a zygosporangium began developing in *d; s,* cross-walls proximally delimiting the paired gametangia; *u,* place of union between gametangia. *E,* Two mycelial hyphae, *a* and *b,* that together have contributed a pair of gametangia whose conjugation has resulted in the young zygosporangium *c;* the hypha *a* further has by itself given rise to the growing zygosporangium *d* by putting forth a pair of sexual branches from positions not far apart. *F,* Hypha with two adjacent intercalary gametangia, *a* and *b,* separated by the cross-wall *s;* after the conjugation tubes extended reciprocally from the gametangia had united at their apices, *u,* the zygosporangium *c* began growing out laterally from *b*. *G, H,* Zygosporangia, each containing an immature zygospore with its spherical protoplast still of granular texture throughout. *I, J,* Zygosporangia, each containing a nearly mature zygospore with two reserve globules in its protoplast. *K–R,* Mature zygospores, each loosely surrounded by the slightly collapsed zygosporangial envelope.

FIG. 3. *Zoöpage pachyblasta;* drawn to a uniform magnification with the aid of a camera lucida; × 1000, except in *B*. *A,* Specimen of *Amoeba* sp. habitually taken by the fungus; two conidia, *a* and *b,* of the fungus are shown adhering to the animal, which contains the nucleus *n* and the contractile vacuole *v*. *B,* Scant arachnoid aerial weft composed of branched ascending conidial chains originating from assimilative hyphae affixed to the three animals *a–c;* × 100. *C,* Proximal portion of aerial hypha, showing above the filamentous part *a* two filamentous conidia, *b* and *c,* representing proximal members of a chain. *D,* Branching aerial hypha still continuous with the part *a,* which while awaiting delimitation as a conidium is supporting two conidial chains that are represented by only the proximal spores *b–k;* one of the chains is branched at the conidium *g,* which accordingly bears a lateral spur. *E,* Intercalary portion of branched chain, showing five conidia, *a–e;* the conidium *b* at the crotch bears a lateral spur. *F,* Intercalary portion of a branched chain, showing six conidia, *a–f;* the conidium *a* at the

crotch bears a lateral spur. *G*, Intercalary portion of branched chain, showing seven conidia, *a–g;* the conidium *b* at the crotch bears a lateral spur near its proximal end, whereas its distal end is bent sideways to form an oblique terminal spur. *H*, Intercalary portion of conidial chain, showing three conidia, *a–c*, in straight alignment. *I*, Detached conidia, *a–z*, showing usual variations in size and shape. *J*, Four widened predaceous hyphae, *a–d*, among untidy remnants of granular protoplasm left scattered about after destruction of a captured *Amoeba; e*, prolongation from a fifth predaceous hypha whose widened part is not shown; *f–i*, young zygosporangia resulting from conjugation of gametangia supplied from the five predaceous hyphae—*f* being traceable backward to *a* and *b*, *g* being traceable to *c* and *d*, *h* being traceable to *b* and *d*, *i* being traceable to *b* and *e; s*, cross-walls proximally delimiting paired gametangia; *u*, place of union between paired gametangia.

FIG. 4. *Zoöpage toechospora;* drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Portion of mycelium with two captured specimens of *Euglypha laevis*, *a* and *b*, each invaded by an assimilative branch; *c*, young erect conidiophore still continuous distally with a series of six young conidia, *d–i*. *B*, Portion of mycelium with two captured specimens of *E. laevis*, *a* and *b*, each of them invaded by an assimilative branch; *c*, *d*, two erect conidiophores, one of them (*c*) still filled with protoplasm and still continuous distally with the series of five young conidia, *e–i*, the other (*d*) almost completely empty and bearing a chain of five mature conidia, *j–n*. *C*, Portion of mycelium with three captured specimens of *E. laevis*, *a–c*, each completely expropriated of contents by an assimilative branch from which the protoplasm has been withdrawn; *d*, *e*, two empty erect conidiophores, one of them (*d*) bearing a chain of four mature conidia, *f–i*, and the other (*e*) bearing a chain of six mature conidia, *j–o*.

FIG. 5. *Zoöpage toechospora;* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, *B*, Portions of prostrate hyphae from each of which an assimilative branch has grown into a captured living specimen of *Euglypha laevis* lying flatwise on the substratum. *C*, Portion of prostrate hypha from which an assimilative branch has grown into a captured living specimen of *E. laevis* resting edgewise on the substratum. *D*, Portion of prostrate hypha from which an assimilative branch has grown into a captured specimen of *E. laevis* lying flatwise on the substratum; the animal seeming near death from loss of protoplasm. *E*, Portion of mycelium from which a separate assimilative branch has grown into each of four captured specimens of *E. laevis*, *a–d*, lying flatwise on the substratum; apparently all four animals have succumbed to death from loss of protoplasm; in *d* withdrawal of contents from the assimilative branch has begun. (Owing to lack of space the main mycelial hypha here is shown in parts, with contiguous ends connected by a broken line.) *F*, Detached conidia, *a–x*, each of which was formed as the terminal member of a chain: *a–h*, individuals with an empty segment at both ends; *i–p*, individuals with two empty segments at the proximal end, and one empty segment at the distal end; *q–s*, individuals with one empty segment at the proximal end, and two empty segments at the distal end; *t–w*, individuals with two empty segments at the proximal end, but distally remaining filled with protoplasm clear to the tip; *x*, distally bifurcate individual with a large empty segment at the proximal

end, and a small empty segment in each of the two divergent arms. *G*, Young unit of sexual reproductive apparatus, showing a nearly full-grown zygosporangium borne on a gametangium that near its tip, *u*, is fused laterally with its mate. *H*, Unit of sexual reproductive apparatus showing origin of paired gametangia from two separate hyphae, *a* and *b*; the wall of the young zygospore is clearly separated from the zygosporangial membrane surrounding it, and is taking on a more undulating contour; the protoplast still fills the zygospore completely, and appears of globuliferous character throughout *I–L*, Units of sexual apparatus wherein the zygosporangial membrane is collapsing about the undulating zygospore wall that loosely envelops a spherical protoplast of globuliferous appearance throughout; in *I* and *K* the origin of the paired gametangia from two separate hyphae is shown. *M*, Nearly mature unit of sexual reproductive apparatus in which the spherical protoplast within the boldly undulating zygospore wall shows a central homogeneous region that is surrounded by globules in smaller number than usual; the place of union, *u*, between the gametangia here appears to be farther from the tip than usual. *N–P*, Mature units of sexual reproductive apparatus, in each of which the undulating zygospore wall within the somewhat collapsed zygosporangial membrane envelops loosely a spherical protoplast that shows a homogeneous central globule surrounded by a globuliferous protoplasmic layer. (*u*, Place of union between paired gametangia.)

FIG. 6. *Zoöpage toechospora;* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, *B*, Portions of mycelium, each bearing an erect young conidiophore, *a*, that is still continuous distally with a series of four young conidia, *b–e*. (Owing to lack of space each continuous erect element is shown in two parts, with contiguous ends connected by a broken line.) *C*, Distal portion of empty mature conidiophore, *a*, showing attachment of a conidium, *b*, representing the lowermost member of a chain. *D*, Distal portion of empty mature conidiophore, *a*, to which is attached the conidium *b*, the lowermost member of a chain. *E*, Portion of empty prostrate hypha bearing two conidiophores, *a* and *b*, from which all protoplasmic contents have been withdrawn and from which all conidia have become detached. *F*, Detached conidium representing the terminal member of a chain. *G* (*a–z*), *H* (*a–g*), Detached conidia representing proximal and intercalary members of chains; all showing a single empty segment at each end.

FIG. 7. Detached conidia of *Zoöpage toechospora* formed as proximal or as intercalary members of chains, and furnished with three or four empty segments; all drawn to a uniform magnification with the aid of a camera lucida; × 1000. *A* (*a–z*), *B*, Specimens showing one empty segment at one end, and two empty segments at the other end. *C*, Detached conidia, *a–c*, each showing two empty segments at each end. *D*, Detached conidia, *a–f*, each showing one empty segment at one end, and three empty segments at the other end.

CYTOLOGY OF THE TELIOSPORES, BASIDIA, AND BASIDIOSPORES OF *SPHENOSPORA KEVORKIANII* LINDER

LINDSAY S. OLIVE

(WITH 4 FIGURES)

INTRODUCTION

The genus *Sphenospora* was founded by Dietel (**1897**), who designated *Diorchidium pallidum* Wint. as the type species. Since then probably only four authentic new species have been described, the most recent of which is *S. kevorkianii* Linder (**1944**). *Sphenospora* is a tropical genus, having been reported in Africa as well as South and Central America.

The rusts of this genus possess subepidermal uredinia and telia, and at times, according to some reports, subepidermal pycnia, all on one host. No aecia and no alternate hosts, if such exist, have been reported for any of its species. The group is particularly characterized by its thin-walled, two-celled, vertically septate teliospores, which germinate upon reaching mature size. Three species have been described on monocots. These are *S. pallida* (Wint.) Dietel, *S. yurimaguasensis* (P. Henn.) Jackson, and *S. kevorkianii* Linder. One species, *S. copaiferae* (P. Henn.) Syd., is parasitic on the legume *Copaifera*. Another species, *S. berberidis* Lagerh., has been described on barberry in Ecuador.

Linder (**1944**) has adequately described the morphology of *S. kevorkianii*. His paper includes accurate illustrations of the rust, particularly of the telial elements. This species is distinguished from all others in the genus by the presence of paraphyses in the telial sorus and in its parasitism of an orchid (*Epidendrum*).

MATERIALS AND METHODS

The material used in the present investigations was very kindly forwarded to me by Dr. Linder, who in turn had received it from Mr. Lewis Long in Nicaragua. The collection consisted of diseased

leaves of *Epidendrum* preserved in formalin-acetic-alcohol solution. The telia were found in various stages of development, the majority containing germinating teliospores. Since the uredinia were old and had finished sporulating, no attempt has been made to study them other than to determine that the urediospores are binucleate.

Some of the material was imbedded in paraffin and sectioned at 7–10 μ. Two methods of staining were used, one being the iron alum haematoxylin technique and the other based on the crystal violet-iodine procedure outlined by Sass (Elements of Botanical Microtechnique, pp. 76–77. McGraw-Hill. **1940**). Orange gold was used as a counter stain in the latter technique and proved particularly useful in bringing out the thin walls of the teliospores and basidia. Each technique had some advantage over the other, and both were needed to give adequate preparations for cytological study.

INVESTIGATIONS

From the standpoint of illustrating and describing all the important stages in nuclear division during the development of the telium, the present work is inadequate. Clear mitotic figures are rare. This is possibly attributable to the condition of the material at the time it was preserved, or to the killing fluid used. It is particularly noticeable that, during phases of nuclear fusion or division, the cytoplasm very frequently absorbs a great deal of the stain, which is almost impossible to remove by destaining. However, enough information has been obtained to follow with reasonable accuracy the cytological development beginning with the production of the teliospore initials and ending with basidiospore formation.

It should be noted here that an examination of the diseased host tissues has revealed the presence of both uninucleate and binucleate haustoria in the cells. The uninucleate ones seemed to be more abundant in the material which I examined.

The telium begins as a palisade of binucleate hyphal tips which aggregate in groups beneath the epidermis. Conjugate nuclear divisions occur in these cells, which may be termed the basal cells, denoting their position in the mature telium (FIG. 1, *1, 2*). Only late anaphase or telophase spindles were observed here and the chromosomes could not be distinguished. The cell produced by a basal cell during this division develops into a teliospore or a pa-

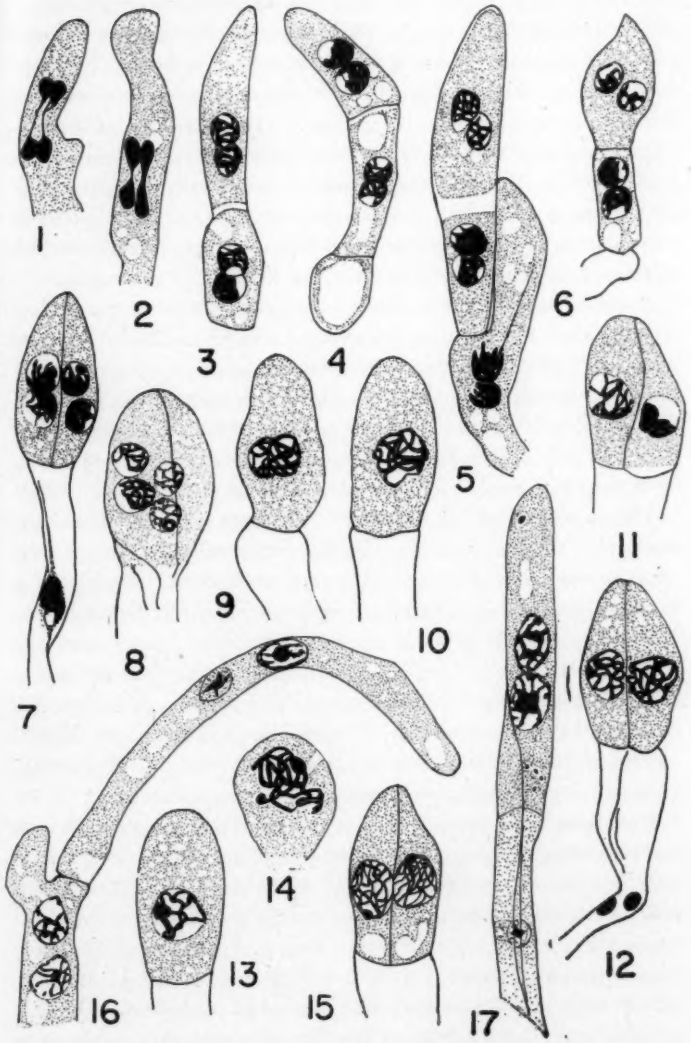

FIG. 1. *Sphenospora kevorkianii.*

raphysis (FIG. 1, *3*). It may therefore be considered a paraphysis initial or a teliospore initial. The two are at first indistinguishable. Other initials may bud out from the same basal cell (FIG. 1, *5, 16*). One basal cell may produce several teliospores and paraphyses, or sometimes only a group of paraphyses. The initial may remain unicellular and develop directly into a one-celled, binucleate paraphysis (FIG. 1, *16; 2, 1, 2*), or less frequently another division may occur to produce a two-celled paraphysis (FIG. 1, *17*). The nuclei in these paraphyses may generally be found to contain distinct nucleoli and radiating bands of chromatin (FIG. *2, 1, 2*).

Many of the initials, probably averaging not over one-half of those produced in a telium, are teliospore initials. Each binucleate teliospore initial divides, evidently with an accompanying conjugate nuclear division, to produce the young teliospore (FIG. 1, *4, 6*). The apical cell becomes the spore proper, whereas the cell beneath it becomes the stalk. Some of the two-celled figures at first cannot be distinguished as paraphyses or teliospores (FIG. 1, *5*).

The apical cell of the young teliospore now undergoes a single division. The two nuclei apparently divide conjugately and their spindles are at right angles to the long axis of the spore, judging from the position of the nuclear pairs following the division (FIG. 1, *7, 8;* 4, *A*). As a result the cross wall is laid down vertically as the apical cell is divided into a two-celled spore. Actual nuclear divisions during this development were rare in the material studied, and the nuclei were generally observed in leptotene, with distinct chromatin bands winding about in the clear interior of nuclear sap. Nucleoli may be frequently observed in these nuclei (FIG. 1, *7, 8*).

Very soon after the two cells are produced the two nuclei in each cell come together and karyogamy takes place (FIG. 1, *9–15*). At this time the chromatin may be in the form of particularly well-defined sinuous bands (FIG. 1, *9, 10, 12*), or sometimes the chromatin strands may clump together during the fusion, so that they are indistinguishable (FIG. 1, *11*). After karyogamy has occurred, paired areas may occasionally be observed along some of the chromatin strands (FIG. 1, *14*). These strands eventually become finer in appearance in the fully developed fusion nucleus, which is now almost the same diameter as the cell it occupies (FIG. 1, *15;* 4, *B*). Each fusion nucleus contains a single nucleolus.

During this development the pedicel of the teliospore elongates considerably, remaining broad above but tapering below. Its cytoplasmic contents disappear and its two nuclei become small and dense, or degenerate completely (FIG. 1, *7, 12*). The mature stalks appear hyaline.

The entire development of the teliospore is similar to that described for *Puccinia,* except that in *Sphenospora* a vertical rather than horizontal cross wall is laid down in the teliospore and the spore wall remains thin. Eventually the maturing paraphyses and teliospores create sufficient pressure upon the overlying epidermis to rupture it; after which the telial elements are exposed and the basidia are produced (FIG. 4, *H, I*).

Shortly after karyogamy has been completed in the teliospore, each of the two cells may germinate apically to produce a basidium. The nucleus and cytoplasm in each cell pass up into the developing basidium. The nucleus is now smaller than it was in the teliospore, but the sinuous chromatin strands are still distinct, as the nucleus remains in leptotene (FIG. *2, 3, 4*). The two basidia generally develop at about the same rate and lie side by side throughout their development. A cross wall may appear at the base of the basidium, or it may fail to appear and then the lower cell of the basidium remains continuous with the teliospore cell. This is indicated in many of the illustrations.

During prophase of the first, presumably meiotic, division of the diploid nucleus in the young basidium, the nucleolus seems to be discharged into the cytoplasm (FIG. *2, 5, 6*). Occasionally two nucleolus-like bodies may be observed in the cytoplasm (FIG. *2, 7, 10*). This may mean that in such cases the two nucleoli of the nuclear pair in the teliospore cell both persisted separately during karyogamy. However, there is no conclusive evidence for this hypothesis. During late prophase the nuclear membrane disappears (FIG. *2, 7*).

A few spindles with chromosomes were observed during the first division (FIG. *2, 8*). In late anaphase and in telophase the chromosomes are indistinguishably clumped together in two dense masses, while the spindle fibers coalesce into one or two dense strands between the two masses (FIG. *2, 9*). The chromatin in each newly formed nucleus generally returns to the leptotene phase with the

characteristic sinuous chromatin strands. In at least a number of cases a nuclear membrane appears around the new nuclei (FIG. 2, *10, 11*). A cross wall may or may not be laid down following this first nuclear division; more frequently it does not appear before the second meiotic division has been completed (FIG. 2, *12–20*).

During the second division, the two nuclei in a basidium generally do not divide quite simultaneously. Again spindles with chromosomes appear and the chromosomes clump together at opposite poles in the later stages of division just as they did in the first division (FIG. 2, *13–17*). The resulting four nuclei are at first dense in appearance and stain darkly throughout (FIG. 1, *18, 20*), but eventually they return to the leptotene condition with distinct chromatin strands and nuclear membranes (FIG. 2, *19*). In neither of the two meiotic divisions was it possible to count the number of chromosomes present.

Typically the first cross wall appears in the quadrinucleate basidium, dividing it into two cells, one uninucleate and the other trinucleate (FIG. 2, *19, 20*). A second wall then appears and divides the trinucleate cell into a binucleate cell and an uninucleate cell, the binucleate cell generally being in the center of the basidium (FIG. 2, *21;* 3, *1a, 2b;* 4, *C*). Occasionally nucleoli are observed in these nuclei (FIG. 2, *21;* 3, *18*). Ordinarily no further cell divisions occur and the basidium germinates directly to produce three basidiospores.

Each cell of the basidium gives rise to a sterigma which enlarges at its tip to produce a single basidiospore. The length of the sterigma is variable, and this is probably correlated with the distance the sterigma must grow in order to expose its tip. The cytoplasm and nucleus in each of the uninucleate cells pass up into the developing basidiospore (FIG. 3, *16*). In the case of the binucleate cell, the cytoplasm and both nuclei pass into the basidiospore (FIG. 3, *13–15, 17*). When a nucleus passes from a basidial cell into the developing basidiospore, it becomes very much attenuated in the region of the sterigma (FIG. 3, *17;* 4, *D*). The migrating nucleus shown in the illustrations revealed three separate strands of chromatin, only two of which could be shown at once, passing through the sterigma.

There is apparently no division of the nuclei in the basidiospores.

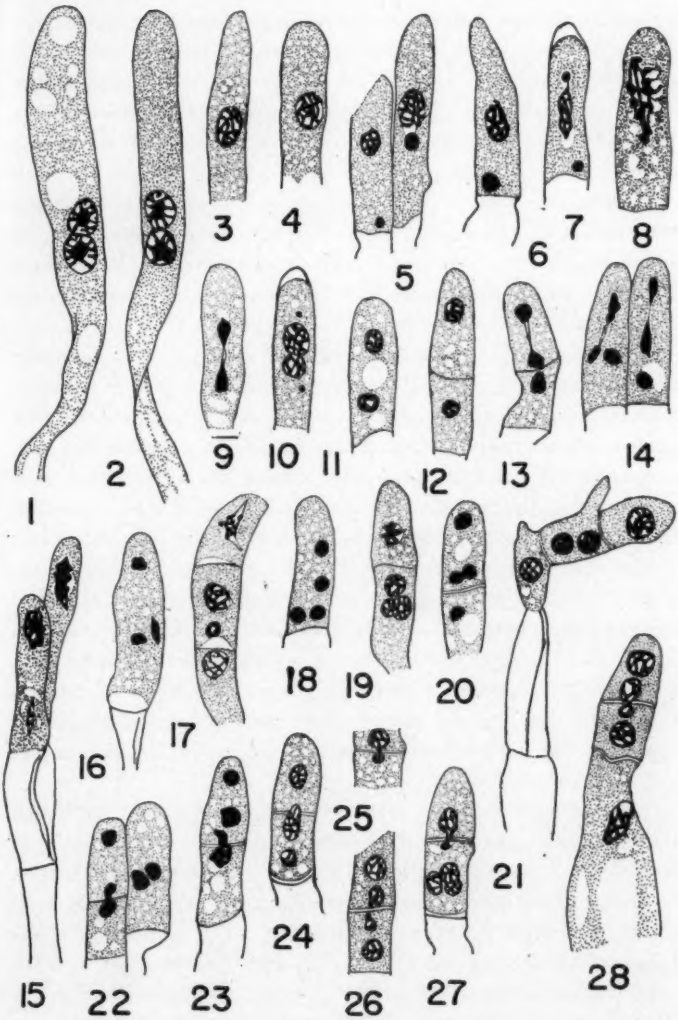

FIG. 2. *Sphenospora kevorkianii.*

The uninucleate spores appear to remain in that condition after they are shed, whereas both nuclei persist in the binucleate spore (FIG. 3, *20*). The uninucleate basidiospores are far more abundant than the binucleate ones. After the nuclei have entered into the basidiospores they return to the leptotene condition, and occasionally a nucleolus may be observed (FIG. 3, *20b*). I have not found any of the basidiospores germinating.

As a result of the absence of any strict correlation between nuclear division and septation in the basidium, several interesting irregularities were observed during the development of some of the basidia. Also a large number of basidial types varying from the one described above were found.

In a considerable number of immature basidia, one of the nuclei occasionally may appear to be migrating through a pore in the cross wall, and this nucleus is usually constricted at the point where it passes through the wall (FIG. 2, *22, 23, 25, 27, 28;* 4, *E–G*). In one basidium, however, a nucleus without any constriction in it was found in the region of the cross wall (FIG. 2, *24*). Another basidium contained a nucleus which had obviously been cut in two by the developing septum (FIG. 2, *26*). Some of the mature basidia were observed to contain five nucleus-like bodies, instead of the usual four, but some of these bodies are abnormally small (FIG. 3, *1b, 2a*). The logical conclusion seems to be that a nucleus, caught in the region of a developing cross wall, has been cut into two parts, and that the nucleus was not migrating through the septum. The fate of these two parts is not known, but the chances are that they disintegrate.

The mature basidia show a great deal of variation. Although they are most commonly three-celled, they may also be two- or four-celled. The distribution of the four nuclei in these basidia is also very variable. Considering the three-celled basidia first, there are several variations of this type. The apical cell or the basal cell, instead of the middle one, may be binucleate and the other two cells uninucleate (FIG. 3, *3, 4*). Such basidia are not very common, however. Other three-celled basidia may contain a single nucleus in each cell, with the fourth nucleus remaining in the teliospore cell (FIG. 3, *7*); or sometimes the teliospore cell may contain a nucleus, one cell of the basidium may be without a nu-

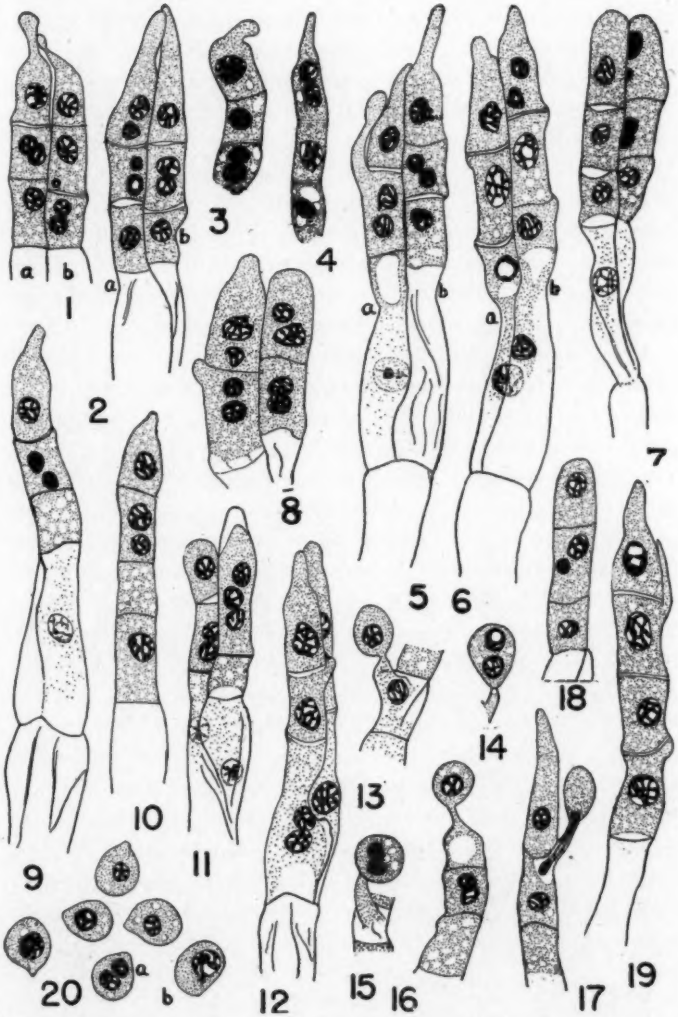

FIG. 3. *Sphenospora kevorkianii.*

cleus, another cell may contain two nuclei, and the third cell may be uninucleate (FIG. 3, *9*). Cells without nuclei have never been observed to germinate. Still other three-celled basidia may have their lowermost cell continuous with the teliospore cell, *i.e.* without a separating cross wall. In this case the nucleus ordinarily present in the lower cell is generally found in the teliospore cell (FIG. 3, *5a*). Rarely a teliospore cell continuous with the lowermost basidial cell may contain two nuclei and then the upper two cells of the basidium are uninucleate (FIG. 3, *12*). All basidial nuclei stranded in the teliospore apparently degenerate, along with the cytoplasm. Therefore, some of the three-celled basidia are capable of producing only two basidiospores (FIG. 3, *5a, 9, 12*).

A few basidia never develop more than two cells. A pair of such basidia were found to contain two nuclei in each cell (FIG. 3, *8*). Another contained three nuclei in the terminal cell with the other cell devoid of a nucleus, the fourth nucleus being in the teliospore (FIG. 3, *11*). Such a basidium would probably produce only a single basidiospore. It is possible that another septum would have appeared later in the trinucleate cell. On the other hand, I have observed a basidium with a uninucleate and a trinucleate cell in the process of germination. The basidium resembled the one shown in fig. 2, *19*, except that the sterigmata had appeared. Presumably the basidiospore produced by a trinucleate basidial cell would also be trinucleate. However, I have not observed such spores.

A four-celled basidium with a single nucleus in each cell, characteristic of most rusts, is a rarity in *Sphenospora kevorkianii* (FIG. 3, *19*). Such a basidium appears capable of producing four basidiospores. This is not true of some of the four-celled basidia, where one of the cells is binucleate and another devoid of a nucleus (FIG. 3, *10*). A single basidium was found to contain five nuclei (FIG. 3, *6*). This may mean that one of the nuclei in the basidium underwent a post-meiotic division.

DISCUSSION

There is a rather striking similarity in the basidial development of *Sphenospora kevorkianii* and *Septobasidium apiculatum* Couch, the development of the latter having been described by me in an

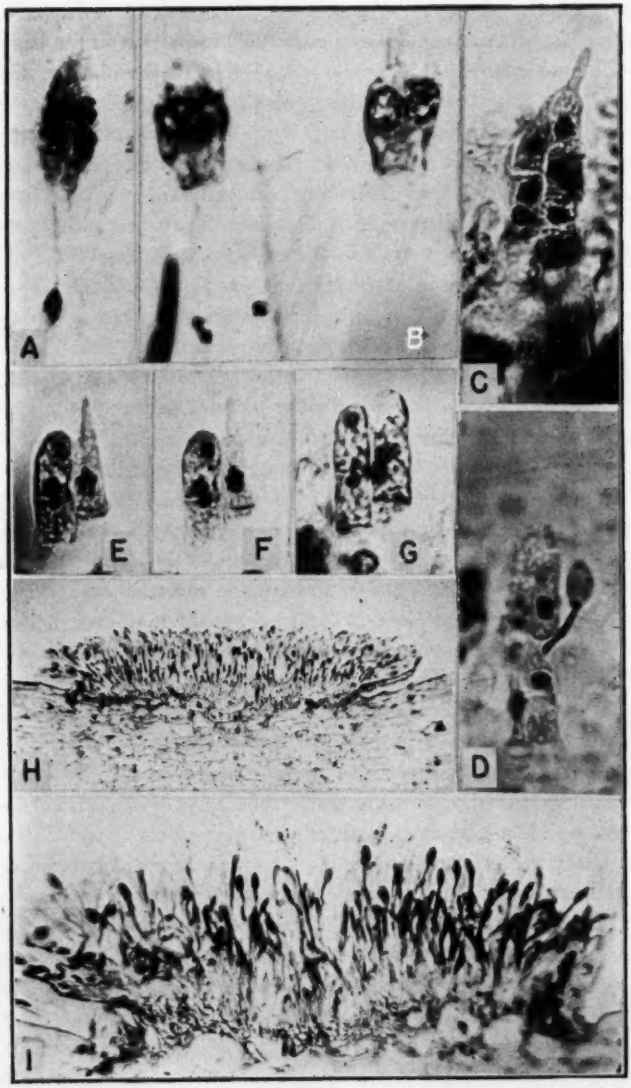

FIG. 4. *Sphenospora kevorkianii.*

earlier paper (**1943**). In both fungi there is often no apparent correlation between meiosis and cross wall formation in the basidium. In *S. apiculatum,* it is the basal cell of the basidium, rather than the middle one, which is generally binucleate; but, as in *Sphenospora kevorkianii,* any one of the three cells may be binucleate and sometimes a four-celled basidium with only uninucleate cells is produced. These two fungi evidently show parallel lines of phylogenetic development, a phenomenon which has been repeatedly observed in the rusts and the Septobasidiales.

The discharge of the nucleolus into the cytoplasm in the prophase of meiosis is not in agreement with what I found in the basidia of *Coleosporium helianthi* (Schw.) Arth. (**1942**). In the latter rust the nucleolus seems to divide into two parts, which probably separate and pass to opposite poles of the spindle. However, in the greater part of the literature on the subject, the nucleolus is more frequently described as being discharged into the cytoplasm, where it disintegrates.

The occurrence of both uninucleate and binucleate basidiospores in *Sphenospora kevorkianii* is of considerable interest. As a result of the manner in which nuclear division and septation occur in the basidium, the binucleate cell is likely to contain most frequently a nucleus from each of the two spindles of the second meiotic division. This further means that the two nuclei are very probably genetically unlike. Therefore, there exists the possibility that such a binucleate basidiospore is capable of producing, upon infection of the host, a dikaryotic mycelium. I have found no record of aecia or of an alternate host for any species of *Sphenospora,* but subepidermal pycnidia have been reported in the genus for the same host that bears the uredinia and telia. It seems probable, therefore, that the rusts of this group are autoecious. However, further research is necessary to establish the validity of this belief. If the rust is capable of leading an autoecious existence, one might expect the basidiospores to be capable of infecting the host. The abundance of uninucleate haustoria, in addition to some binucleate haustoria, in leaves of *Epidendrum* diseased by *S. kevorkianii* indicates that this is the case. Leaves of the orchid have not been inoculated with basidiospores of the rust, and no further evidence is available regarding their ability to infect the host.

In considering the possible phylogenetic origin of the fungus and its taxonomic position, a comparison might well be made first with the more familiar development of teliospores and basidia in *Puccinia* (Allen, **1933**). The teliospores of the two rusts develop in essentially the same manner, except that in *Sphenospora* the septum dividing the spore into two cells is vertical instead of horizontal, and the spore wall does not thicken as in *Puccinia*. However, some species of *Puccinia*, such as *P. boutelouae* (Jennings) Holw., *P. levis* (Sacc. & Bizz.) Magn., and *P. flaccida* B. & Br., may have teliospores with septa varying from horizontal or oblique to vertical.

The genus *Diorchidium* Kalchbr. has a type of teliospore which appears to bridge the gap between the *Puccinia* and *Sphenospora* types. Here the teliospore is divided into two cells by a vertical septum, and the spore wall is typically thickened and brownish, instead of thin and hyaline as in *Sphenospora*. The species of *Puccinia* mentioned above produce some teliospores which intergrade with those found in *Diorchidium*. But in at least one species of *Diorchidium, D. piptadeniae,* the spore wall is only moderately thickened and pale in color. On the other hand, in *Sphenospora berberidis,* which is a rather atypical species, the teliospore wall becomes thickened above and is pale cinnamon in color. Even Dietel (**1903**), who founded the genus *Sphenospora,* later expressed some doubt as to whether this genus would stand. His observations on *D. piptadeniae* were responsible for this later view. Saccardo did not recognize *Sphenospora* as a valid genus, and he placed species described under that name in *Diorchidium*. Dietel (**1928**) finally placed *Sphenospora* in the tribe Ravenelieae of the Pucciniaceae.

Arthur (**1925**) assigned *Sphenospora* to the subfamily Skierkatae of the Aecidiaceae (Pucciniaceae) along with *Skierka, Ctenoderma,* and *Chaconia*. Its relationship with these last mentioned genera is obscure. *Skierka* and *Ctenoderma* have unicellular teliospores with deciduous pedicels; whereas *Chaconia* has sessile teliospores arising singly or in groups from enlarged basal cells in the telium.

Cummins (**1941**) suggests that *Sphenospora* may be related to *Ypsilospora*. He describes the latter genus as having unicellular

teliospores in pairs at the tips of common pedicels. He further states that the arrangement of the two teliospores on a common pedicel is similar to the condition found in *Sphenospora,* except that the two spores have no common wall. Cummins attempts to strengthen this view with Sydow's description (**1924**) of the teliospores of *S. copaiferae* as ". . . am Septum meist ziemlich tief eingeschnurt," which apparently means that the two cells of the teliospore remain attached along the septum below but tend to separate above. This phenomenon occurs quite commonly in *Gymnosporangium,* where the cells of the teliospore often tend to separate at the septum after the spore has been in water for some time.

Linder (**1944**) appears to agree with Cummins that *Sphenospora* is allied to *Ypsilospora* by virtue of these similarities in teliospore development. However, such comparisons seem to me to be based more upon analogies than homologies. The description of *Ypsilospora* indicates that two one-celled teliospores arise independently at the apex of a common pedicel and that each remains unicellular. In *Sphenospora* a teliospore initial divides to produce two cells, one of which is the pedicel and the other the spore proper. This latter cell would appear to be homologous with *one* of the unicellular teliospores in *Ypsilospora,* although it later becomes two-celled by the formation of a vertical septum. It is possible that the so-called pedicel in *Ypsilospora* is homologous with the basal cell in the telium of *Sphenospora* and that the two spores produced at its apex are actually sessile. However, further developmental studies on the teliospores of *Ypsilospora* are needed before any conclusive comparisons based upon homologies can be made.

I feel that, until more extensive cytomorphological investigations have been made on other genera of rusts seemingly related to *Sphenospora,* the genus should be retained as a member of the tribe Ravenelieae of the Pucciniaceae, as previously designated by Dietel. In actuality, its teliospore development probably has more in common with the development in *Puccinia* than with that in *Ravenelia.* Therefore, it may later prove advisable to erect a new and intermediate tribe to include such genera as *Sphenospora* and *Diorchidium.*

SUMMARY

1. The cytomorphological development of the teliospores of *Sphenospora kevorkianii* is essentially like that described for *Puccinia,* except that the spore septum is vertical and the spore wall remains thin. At maturity each cell contains a single large fusion nucleus.

2. Paraphyses are produced in large numbers from the same cells in the telium that produce the teliospore initials. They are generally unicellular and binucleate, but are sometimes two-celled.

3. Each cell of the teliospore germinates to produce a basidium apically. Two meiotic divisions take place in the basidium, the nucleolus being discharged into the cytoplasm during the first division.

4. Four nuclei are produced in the developing basidium, which generally becomes three-celled, with one nucleus in each of two cells and two nuclei in a third cell. The septa are produced in an irregular manner, generally not directly correlated with the nuclear divisions.

5. Two- and four-celled basidia are also produced.

6. Some of the nuclei in the developing basidia appear to be cut into as they get in the way of the developing septa.

7. Mature basidia produce from one to four basidiospores, usually three. Spores produced by uninucleate cells of the basidium are uninucleate. Those produced by the binucleate cells are binucleate. There appears to be no nuclear division in the basidiospores at this time.

8. The taxonomic treatment of the genus *Sphenospora* by Dietel seems to be the most acceptable at present. Thus the genus is retained in the tribe Ravenelieae of the Pucciniaceae.

The author is very grateful to Dr. C. W. Edgerton, who made the photographs for this paper.

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EXPLANATION OF FIGURES

FIG. 1, *1–17* (all figures × 1410). *1, 2,* basal cells with nuclei dividing conjugately; *3,* basal cell and initial cell; *4,* young teliospore with pedicel; *5,* young teliospore or paraphysis, basal cell budding out second initial; *6,* young teliospore with pedicel; *7, 8,* two-celled teliospores just after conjugate nuclear division; *9, 10,* two cells of same teliospore, showing nuclear fusion; *11–13,* stages in nuclear fusion in the teliospore; *14,* crushed teliospore with fusion nucleus (note nucleolus); *15,* mature teliospore with fusion nucleus in each cell (note nucleoli); *16,* unicellular, binucleate paraphysis; basal cell budding out a new initial; *17,* two-celled paraphysis.

FIG. 2, *1–28* (all figures × 1410). *1, 2,* mature binucleate paraphyses; *3, 4,* young basidia, each with fusion nucleus in leptotene; *5, 6,* prophase of first meiotic division, nucleolus being discharged into cytoplasm; *7,* late prophase with two nucleolus-like bodies apparently being discharged into the cytoplasm; *8,* anaphase spindle of first meiotic division; *9,* telophase of first meiotic division; *10,* binucleate basidium with two nucleolus-like bodies appearing in the cytoplasm; *11,* binucleate basidium; *12,* binucleate basidium with cross wall; *13–17,* stages in second meiotic division; *18,* unicellular, quadrinucleate basidium; *19, 20,* quadrinucleate basidium with single septum; *21,* mature three-celled basidium; *22–28,* nuclei in the region of the cross walls of the basidia.

FIG. 3, *1–20* (all figures × 1410). *1–7,* various types of three-celled basidia; *8,* a pair of two-celled basidia; *9,* three-celled basidium with one cell devoid of a nucleus; *10,* four-celled basidium with one cell lacking a nucleus; *11,* two-celled basidium with one cell empty and one containing three nuclei; *12,* three-celled basidium with lower cell continuous with the teliospore cell, the latter containing two nuclei; *13–15,* germination of binucleate basidial cells to produce binucleate basidiospores; *16,* uninucleate cell producing a uninucleate basidiospore; *17,* nucleus of binucleate cell passing up into basidiospore; *18,* basidial nuclei showing nucleoli; *19,* four-celled and quadrinu-

cleate basidium; *20*, basidiospores, one binucleate (a) and one showing nucleolus (b).

FIG. 4, *E–I*. Photomicrographs. *A*, two-celled teliospore immediately after conjugate nuclear division. Note the two nuclei in each cell (also *see* FIG. 1, *7*). *B*, two-celled teliospores with a single fusion nucleus in each cell. *C*, mature basidia germinating (*see* FIG. 3, *5*). *D*, nucleus passing from binucleate cell of basidium into basidiospore (*see* FIG. 3, *17*). *E–G*, basidial nuclei in the region of the septa, *E* and *F* representing the same at slightly different levels. *H*, *I*, vertical sections through the telia, showing paraphyses, teliospores, and basidia. (*A–G*, × 1075; *H*, × 65; *I*, × 100.)

THE PRODUCTION OF SPORES IN SUBMERGED CULTURES BY SOME STREPTOMYCES [1]

FERNANDO CARVAJAL [2]

(WITH 7 FIGURES)

Foster et al. (2) reported the formation of submerged spores in shaken and aerated cultures of *Penicillium notatum* and *P. chrysogenum*, which previously had been known to form spores only on the aerial mycelium. This sporulation was first indicated to them by an insoluble greenish pigmentation which settled out with the other solid material from the broth. Microscopic examination of this material showed that typical conidiospore formation had occurred in the submerged cultures and that the green pigment was due to the presence of a considerable number of these spores.

Sporulation of microorganisms belonging to the genus *Streptomyces* is usually thought of as occurring on the aerial mycelium. The formation of spores in submerged cultures by species of *Streptomyces* has not been noted previously. In the course of mycological studies in connection with the production of streptomycin, submerged sporulation has been observed by the writer. A description of this phenomenon, which is also illustrated with microphotographs, comprises the subject of the present communication.

The various fermentation samples studied were from large fermenters and shake flasks maintained at 75° F.

The following streptomycin producing strains of *S. griseus* were used in these experiments: SL no. 842, SL no. 842–4, FC no. 2103, FC no. 1196 (all isolated from soil samples by the writer), and *S. griseus* no. 4 from Dr. S. A. Waksman. One non-streptomycin producing strain, *S. griseus* FC no. 3077, and other Actinomycetes such as *Streptomyces lavendulae* SL no. 752 (streptothricin pro-

[1] Presented before the Mycological Society of America at Boston, Massachusetts, December 26–30, 1946.

[2] Contribution from Schenley Laboratories, Inc., Research and Development Division, Lawrenceburg, Indiana.

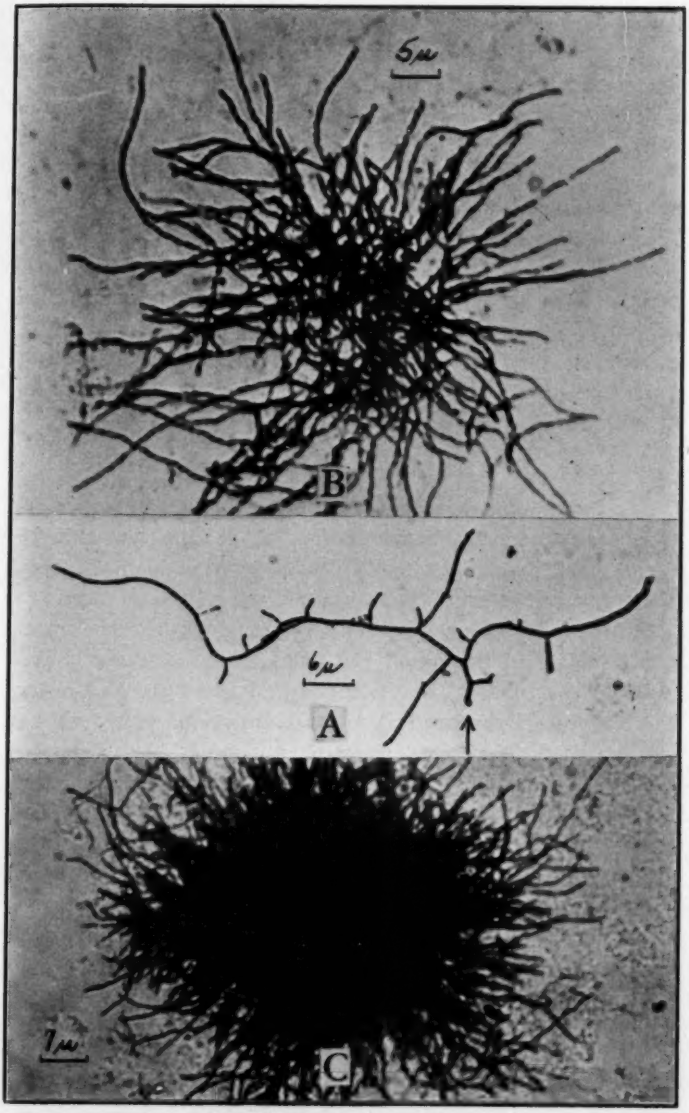

FIG. 1. *Streptomyces griseus.*

ducer); *Streptomyces* sp. FC no. 2969 and *Actinomyces albus* ATCC no. 618 (Krainsky's type species) were also employed in these tests.

Slides were prepared by drying smears of fermentation broth at room temperature, staining with Loeffler's methylene blue or with Poirrier's cotton blue, washing (to remove excess stain), drying, and then affixing the cover slips with Canada balsam.

When permanent slides were prepared from the aerial growth of sporulated colonies on the surface of the agar (FIG. 6*A* and *B*), a loop containing distilled water was moved over the colony. Then the film of water containing aerial mycelium spores in chains, etc. was smeared on a clean slide, fixed and stained. Mycelium and spores of the same strain of the organism grown in different media often showed different affinity for the stain.

SPORE PRODUCTION IN SUBMERGED LIQUID CULTURES

The fungus, *S. griseus,* undergoes certain morphological changes in submerged, aerated, liquid cultures which culminate with the completion of its life cycle by the production of submerged spores. The manner of spore formation in submerged cultures of *S. griseus* strains is much the same as that which occurs on the aerial mycelium on solid or liquid media (1). The spores are easily broken loose at their points of attachment and go into suspension in the agitated broth. In spite of the agitation brought about by stirring and aeration, long spore chains are often found in the broth (FIGS. 3, 4 and 5*A* and *B*). These spore chains probably are not fully mature; consequently they are quite resistant to breakage. The spores are of various shapes, mainly: oval, cylindrical, spherical, bean, or barrel shaped (FIGS. 3, 4, and 5).

The spores may be produced on sporogenous branches (FIG. 3, *B*), at the tips of vegetative mycelium, mycelial fragments may become entirely sporogenous (FIG. 4), a considerable part of the vegetative mycelium may become fertile (FIG. 5*A* and *B*), or spores may be formed in the germ tubes of germinating spores (FIG. 5*D*). The specialized sporogenous branches (FIG. 3*B*) are often clavate when young and arise from the mycelium usually singly or sometimes in groups of two or more from a single position on the mycelium. Many sporogenous branches may also arise from a single

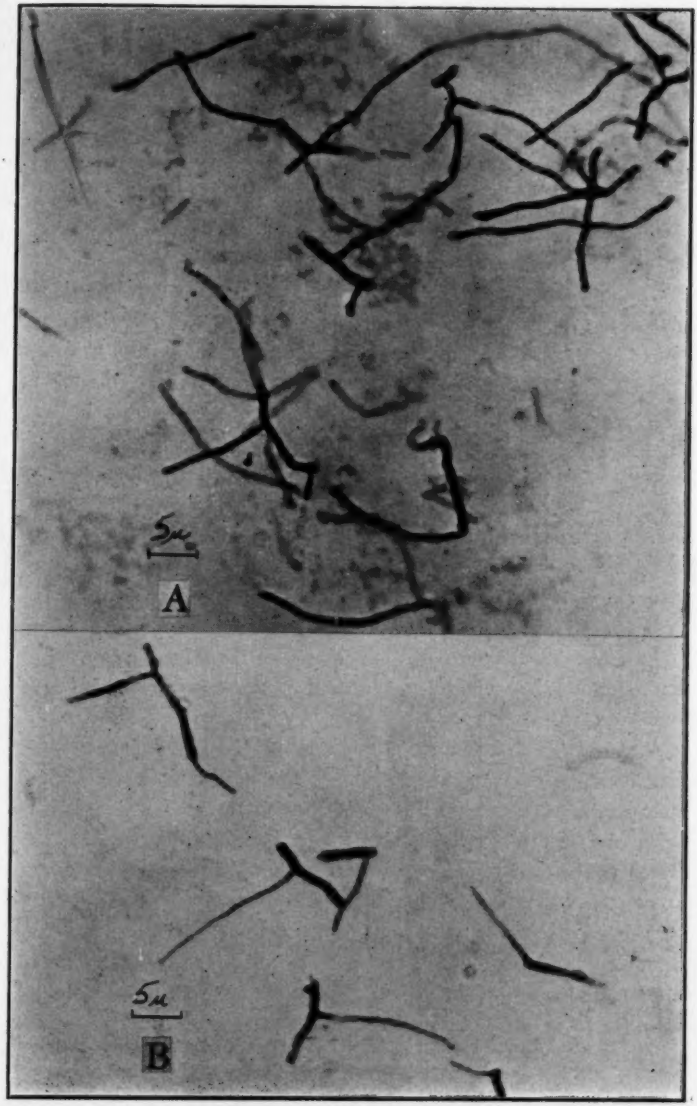

FIG. 2. *Streptomyces griseus.*

hypha. The point of attachment of sporogenous branches in fertile mycelium may be an apparently normal spore or one of irregular size and shape, *i.e.* T-shaped or triangular (FIG. 5*A* and *B*). One or more side chains may be attached to these spores so that the main axis and the secondary branches appear as a network of spores. Sometimes empty spaces are found between spores in the same spore chain. These empty spaces often appear to be collapsed and flattened so that the diameter appears to be larger than that of the rest of the spore chain.

The physiological and morphological characteristics of submerged spores and aerial spores appear to be similar. The submerged spores germinate normally by means of one to several germ tubes (FIG. 5*C*), and streptomycin production by the resulting thallus corresponds to that of the parent culture.

Production of spores in submerged cultures was not limited to strains of *S. griseus*. The morphological changes noted in submerged cultures of *S. griseus* were also observed (FIG. 6*C*, *D*, *E*, and *F*) in similar cultures of the following organisms: *Streptomyces lavendulae*, *Streptomyces* sp., a chromogenous type, and *Actinomyces albus* Krainsky (3) (*Streptomyces albus* [Krainsky] Waksman and Henrici).

Although the above organisms produce aerial spores in spiral chains, the spore chains produced in submerged cultures were straight (FIG. 6).

A. *Tank Fermentations*. The samples for examination were usually taken every twelve hours. During the first twelve hours after seeding of the broth with spores of *S. griseus*, the spores germinated and produced a typical fungous thallus (FIG. 1*A*). Between twelve and twenty-four hours they produced a considerable amount of mycelium which was rich in protoplasmic contents. Mycelial growth was quite rapid from 24 to 48 hours. The mycelium continued to produce new branches and at the same time vacuolation and empty portions in the mycelium appeared as empty tubes in fresh and in stained preparations (FIG. 2*A* and FIG. 3*A*).

There was some indication that the mycelium had broken at the empty spaces since fragments often were found with empty and collapsed ends both of which were separated from the turgid area by septa. Scattered mycelial fragments also were found through-

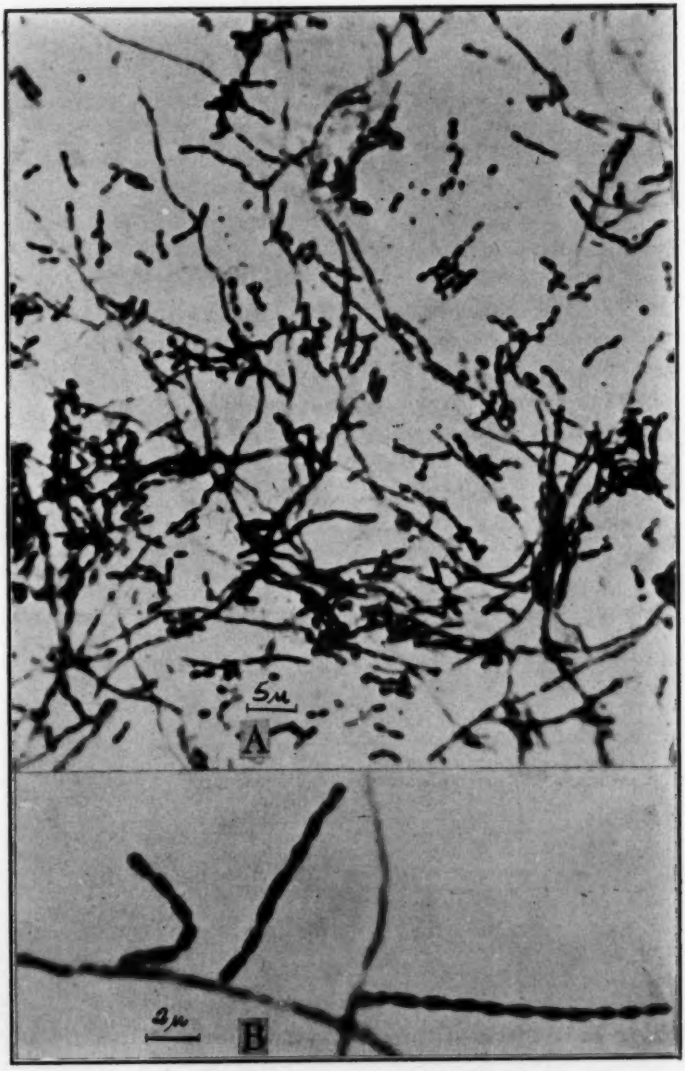

FIG. 3. *Streptomyces griseus.*

out the broth (FIG. 2, *A*). These mycelial fragments might germinate at any place by one to several germ tubes (FIG. 2, *B*) similar to those produced by the spores (FIG. 5, *C*), or they might produce spores (FIG. 4). Although disintegration of the mycelium occurred during fermentation, especially from 36 to 84 hours, a large number of submerged spores were usually produced at the same time.

In some instances little or no mycelium could be found in the broth but the presence of large numbers of viable spores was evident. These submerged spores could germinate in the same broth and produce new mycelium. The submerged spore production might start within twenty-four to sixty hours after the fermenters were seeded.

The life cycle of *S. griseus* was repeated if the fermenter was kept for 70 to 100 or more hours (TABLE II).

The following tables I and II are typical examples of fermentations using two different media.

Table I is typical of fermentations using corn steep liquor me-

TABLE I

SUBMERGED SPORE PRODUCTION AND MYCELIAL GROWTH OF S. GRISEUS IN LARGE FERMENTERS IN CORN STEEP LIQUOR MEDIUM

Fermentation Samples Time	Stage of Growth	pH	Streptomycin Activity (*mcg./ml.*)
0 hours	Original spores	7.2	0.0
12–24 hours	Spores germinating and developing a considerable amount of mycelium	6.78	0.0
36 hours	Mycelium profuse. Some vacuolation and empty portions in mycelium.	7.18	4.0
48 hours	Mycelium profuse. Some fragmentation and some cellular disintegration of mycelium evident. A few submerged spores produced.	7.02	55.0
60 hours	Fragmentation and disintegration of mycelium increasing. Considerable amount of submerged spores produced.	7.18	189.0
72 hours	Considerable fragmentation and disintegration of mycelium. Great amount of submerged spores produced.	7.28	250.0
84 hours	Considerable fragmentation and disintegration of mycelium. Profuse submerged sporulation. Some spores germinated.	7.23	250.0
88 hours	Similar to 84 hours but more sporulation and more spores germinated.	7.32	250.0

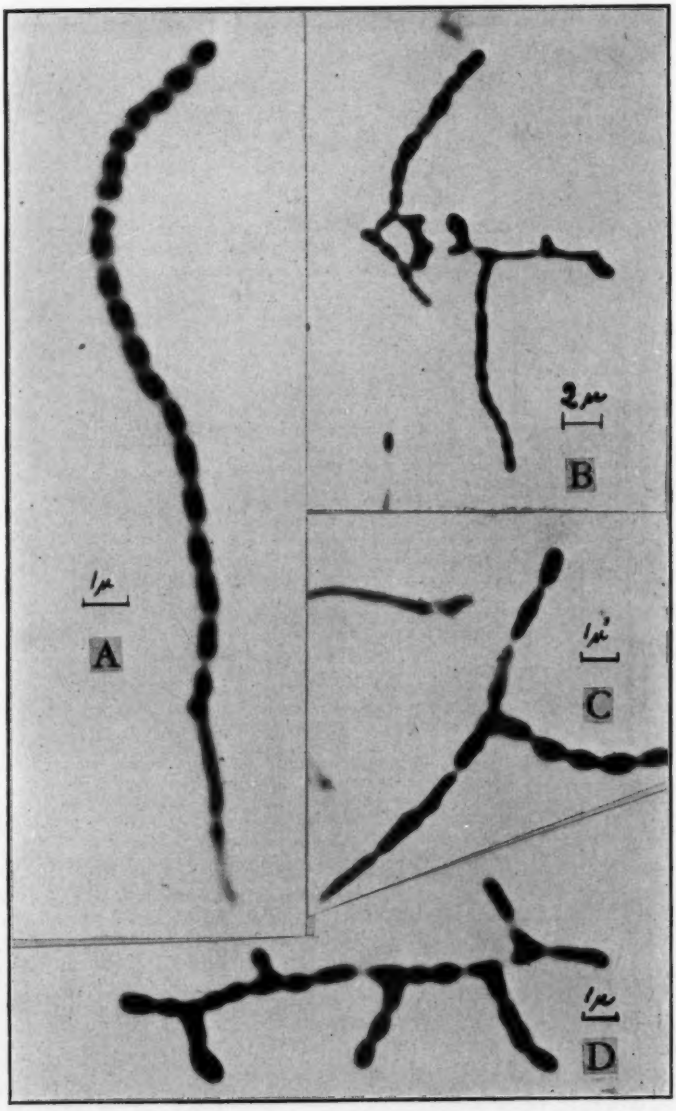

FIG. 4. *Streptomyces griseus.*

dium. In this medium when submerged sporulation started streptomycin production rose rapidly.

Table II is typical of fermentations in a tank using synthetic medium. It appears that good submerged sporulation occurred before any streptomycin was produced.

TABLE II

SUBMERGED SPORE PRODUCTION AND MYCELIAL GROWTH OF S. GRISEUS IN LARGE FERMENTERS IN SYNTHETIC MEDIUM

Fermentation Samples Time	Stage of Growth	pH	Streptomycin Activity (*mcg./ml.*)
0 hours	Original spores	7.48	0.0
12 hours	Spores germinating and developing a considerable amount of mycelium. Some vacuolation and empty portions in mycelium observed.	7.61	0.0
24 hours	Mycelium well developed and some fragmentation and disintegration of mycelium accompanied the production of a considerable number of submerged spores.	7.28	0.0
36–48 hours	Heavy sporulation evident and vegetative mycelium almost completely disappeared. Many spores germinated and others swollen.	7.32–7.22	0.0
60 hours	Greater sporulation evident and new mycelium developing from new spores.	7.06	9.0
72 hours	Heavy sporulation present and good mycelium developing from new spores.	6.93	16.0
84 hours	New mycelial growth increasing in amount, spore count decreasing greatly.	7.48	39.0
96 hours	New mycelium very profuse, rich in protoplasm and a very few spores evident.	7.29	85.0
108 hours	Large amount of sporulation evident; very little vegetative mycelium present.	7.21	87.0
120 hours	Sporulation increased over that evident at 108 hours. Mycelium almost absent.	7.09	158.0
132 hours	Amount of sporulation increased, mycelium practically all gone. Spores germinating and producing more spores at their tubes and young mycelial branches.	6.90	95.0

A greater submerged sporulation was produced in a shorter time of fermentation in synthetic medium than in the corn steep liquor medium. The relationship between the increase in submerged sporulation and streptomycin production depends largely on the type of medium used.

B. *Shake Flask Cultures.* Several experiments were carried out with shake flask cultures grown in 500 ml. Erlenmeyer flasks, each

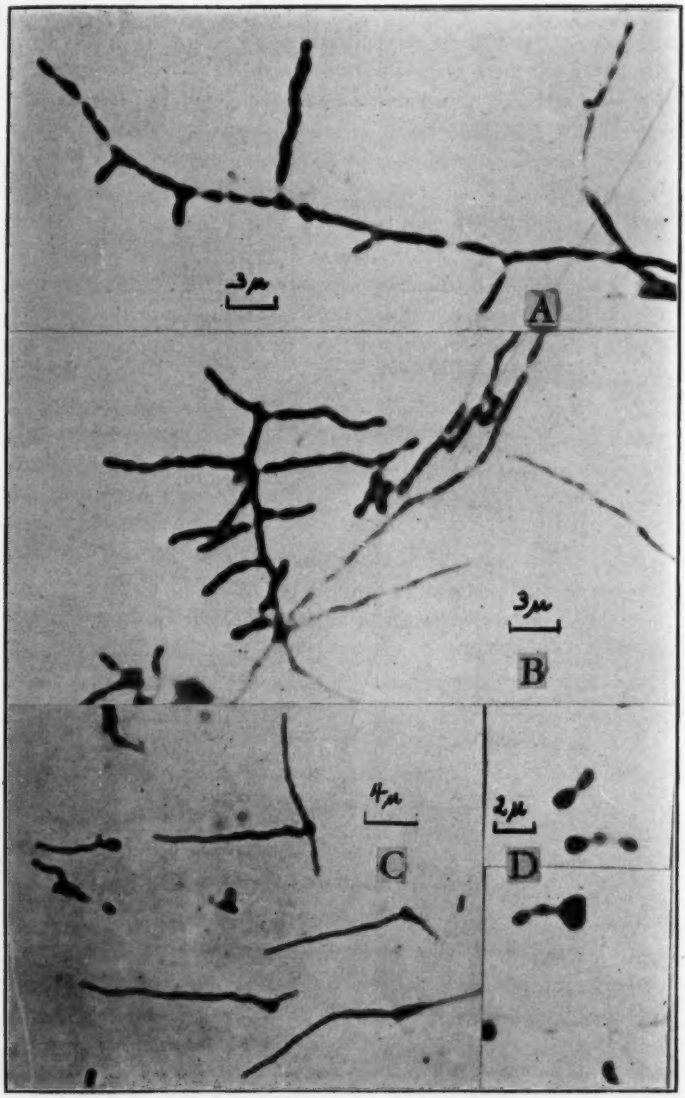

FIG. 5. *Streptomyces griseus.*

containing 100 ml. of medium which had been seeded with 1 ml. of spore suspension in sterile water. In order to avoid aerial growth of mycelium on the sides of the flasks and spore formation from such growth, the contents of each flask were transferred daily to another clean, sterile flask. Each flask was also shaken by hand several times during the day and its position in the shaker changed by a quarter turn. Good results were obtained with the following media. 1. Corn steep liquor 15.0 ml. per 1000 ml. of distilled or tap water. 2. Beef extract (Difco) 7.0 gm. per 1000 ml. of distilled or tap water 3. Dextrose 10.0 gm., peptone 5.0 gm., beef extract 3.0 gm., NaCl 5.0 gm. per 1000 ml. of distilled or tap water. 4. Dextrin 25 gm., peptone 5.0 gm., beef extract 3.0 gm., NaCl 5.0 gm. per 1000 ml. of distilled or tap water.

S. griseus in shake flask cultures was observed to undergo morphological changes similar to those which occurred in the large fermenters; however, in the shake flasks the process was usually much slower. Good sporulation usually occurred at ages of two to six days.

In a modification of Foster's medium: manioc 20.0 gm., $NaNO_3$, 6.0 gm., KH_2PO_4 1.5 gm., $MgSO_4 \cdot 7H_2O$ 0.5 gm., $CaCl_2$ 25.0 gm., tap water 1 liter, the formation of loose mycelial wefts (FIG. 1*B*) and of a large amount of compact pellets (FIG. 1*C*) occurred from 1 to 3 days; however, subsequent submerged spore production was very poor.

A non-streptomycin producing strain, *S. griseus* FC no. 3077, in shake flasks produced better sporulation in 1 to 3 days than any of the *S. griseus* streptomycin-producing strains did under identical conditions.

SUBMERGED COLONIES OF S. GRISEUS IN SOLID NUTRIENT AGAR

The strains of *S. griseus* employed in this work readily sporulated in completely submerged colonies in nutrient agar (dextrose 10.0 gm., peptone 5.0 gm., beef extract 3.0 gm., NaCl 5.0 gm., agar 15.0 gm., water 1000 ml.) in Petri plates at pH 7.0, at room temperatures (75–85° F.). Good spore formation has been observed two to twelve days after seeding the agar with spores.

The submerged sporulated colonies were circular, nearly colorless and opaque; concentric-growth rings and sectors often appeared

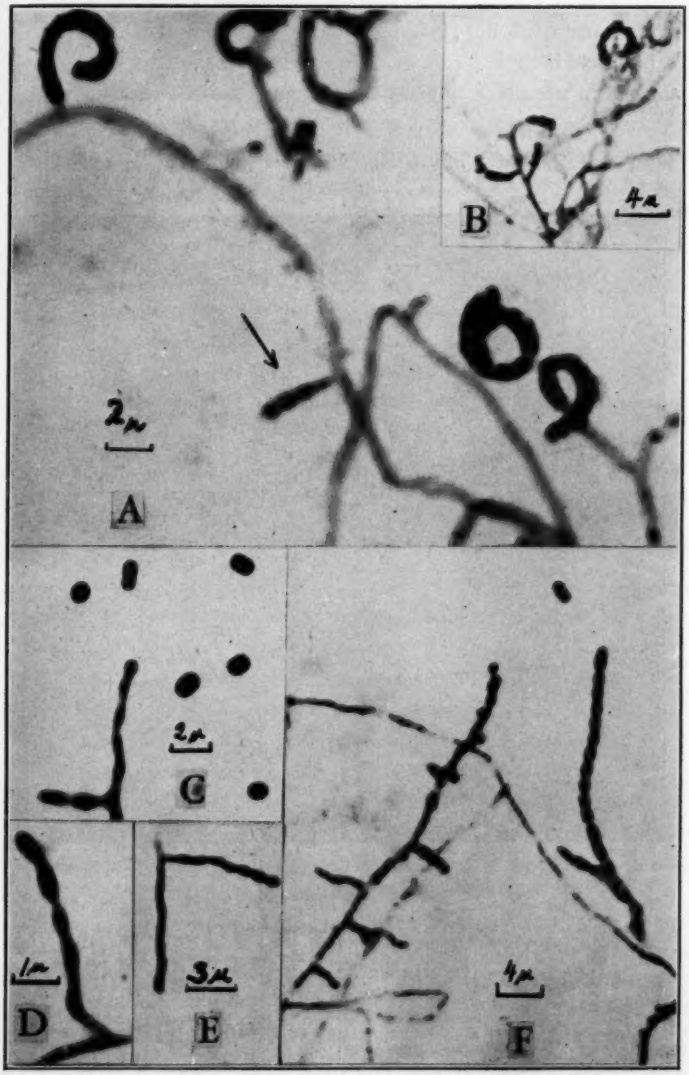

FIG. 6. Spore formation in species of *Streptomyces*.

after several weeks. In submerged well-sporulated colonies, it was often difficult to find typical mycelium since almost all of the mycelium had become fertile or disintegrated. Here, the spores were formed in a manner similar to that found in submerged liquid cultures. Very long spore chains were often produced (FIG. 7) and the mature spores might germinate and develop normal mycelium or secondary spore chains. Submerged mycelium of *S. griseus* no.

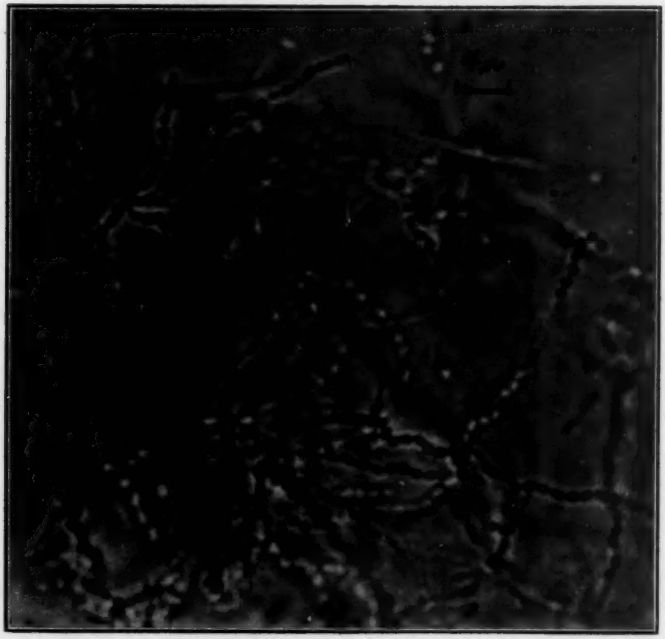

FIG. 7. Spore formation in *Streptomyces griseus* on solid media.

SL 842 produced spores in a shorter period of time than the other *S. griseus* strains under identical conditions. Crowded colonies sporulated in a shorter time than did the well separated ones.

The study of submerged colonies of Actinomycetes in solid medium might be advantageous in cytological work on nuclear behavior, septation, reproduction, etc. The spores and mycelium in all stages are well preserved *in situ*, they stain very well and show the

cytoplasmic contents clearly. Smears and microtome sections of this material are easily prepared.

SUMMARY

1. Information on the life cycle of the fungus *S. griseus* in submerged cultures is reported. The spores first germinated and produced profuse vegetative and typical fungous mycelium. Vacuolation, fragmentation and cellular disintegration of the mycelium was evident during fermentation in deep cultures, accompanied usually by the formation of large numbers of spores.

2. Submerged spores could be produced in a shorter time and in much larger quantities than spores produced on the aerial mycelium on the surface of solid or liquid media.

3. The mycelial fragments may germinate at any place by one to several germ tubes, similar to those produced by the spores.

4. In some instances at a certain age of fermentation, little or no mycelium was found in the broth; but the number of viable spores was profuse.

5. Submerged spore production may start within twenty-four hours after the fermenters are seeded. The submerged sporulation in large fermenters usually appears in a shorter time than in shake flasks.

6. All the *S. griseus* strains studied produced spores in submerged cultures. Some differences were found among strains in regard to the time and amount of sporulation.

7. The spores were found to be formed in chains: (1) In sporogenous branches arising from the vegetative mycelium; (2) at the tips of vegetative mycelium; (3) in the mycelium, in the main axis and secondary branches; (4) in mycelial fragments; and (5) in the germ tubes of spores and mycelial fragments.

8. The spores produced in submerged cultures were smooth and wettable. The physiological and morphological characteristics of submerged spores and of the aerial spores produced on the mycelium on solid or liquid media were similar.

9. Other species of the genus *Streptomyces, S. lavendulae, S. albus* and a *Streptomyces* sp., produced submerged spores in deep cultures. The morphological changes exhibited by these organisms during fermentation were very similar to those of *S. griseus* strains.

10. Colonies of *S. griseus*, submerged in nutrient agar, produced a large number of spores within two to twelve days at room temperature.

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DESCRIPTION OF FIGURES

FIGURE 1. *Streptomyces griseus* No. 2103, submerged cultures. A. Young thallus developing from single spore (arrow). B. Mycelial weft from a 48 hour culture. C. A compact pellet from a 48 hour culture.

FIGURE 2. *S. griseus* No. 2103, 48 hour submerged culture. A. Fragmented mycelium. Note empty portions of mycelium. B. Six mycelial fragments germinating by germ tubes.

FIGURE 3. *S. griseus* No. 2103, 60 hour submerged culture. A. Submerged spore formation and vegetative mycelium. B. Young spore chains borne on vegetative mycelium.

FIGURE 4. *S. griseus* No. 2103, 60 hour submerged culture. A. Young spore chain, note differences in size and shape of spores. B, C, and D. Spore chains. Note size and shape of spore connecting different spore chains.

FIGURE 5. *S. griseus* No. 2103, 60-hour submerged culture. A and B. Spore formation throughout the ramified mycelium including the main axis and secondary branches. Note (A) spores connecting different branches. C. Germination of submerged spores by 1–3 germ tubes. D. New spores produced at germ tubes of recently germinated spores.

FIGURE 6. Other Actinomycetes. A and B. *Streptomyces* sp. No. 2969. Aerial spore formation. A. A young clavate and septate sporogenous hypha (arrow) rising from the vegetative mycelium. Note curled spore chains. B. Formation of aerial spore in clavate and twisted sporogenous branches and their relation to the vegetative mycelium. C. *Streptomyces* sp. No. 2969. Submerged spore formation. Young spore chains and ripened scattered spores. D and E. *Streptomyces albus* (ATCC No. 618). Submerged spore formation. D. Young sporogenous hypha born on vegetative mycelium. E. Young spore chains. F. *Streptomyces lavendulae* No. 752. Submerged spore formation and its relation to the vegetative mycelium.

FIGURE 7. Production of submerged spores of *S. griseus* No. 2103 in solid nutrient agar after 6 days. One spore (arrow) connecting spore chains to the main axis. From unstained and living preparations.

NEW OR OTHERWISE NOTEWORTHY SPECIES OF TUBERALES

HELEN M. GILKEY

(WITH 17 FIGURES)

Since the publication in 1939 of Tuberales of North America, the author has had opportunity to study further collections of fungi belonging to this order and the gleanings from these investigations are recorded in the following notes. They include one new genus, four new species, a new interpretation of a former species, and considerable extension of range for certain previously known members of the Tuberales.

The types of all new species are deposited at Oregon State College.

Caulocarpa gen. nov.

Ascomatibus carnosis, stipitatis, lente lobatis; interiore in cava partito, parietibus cavorum hymenio praeditis; gleba lacunis ad ascomatis superficiem apertis praedita; ascis cylindricis, octosporis; paraphysibus exilibus; sporis uniseriatis, levibus.

Ascocarp fleshy, stipitate, somewhat lobed, internally separated by partitions into hollow, hymenium-lined chambers opening to surface at furrows between lobes; asci long, slender, eight-spored; paraphyses equaling asci, narrow, septate, not swollen at apex; spores uniseriate, ellipsoid, small, smooth.

The genus *Hydnotrya* has previously been expanded by the present writer to accommodate several American entities which, although differing widely in certain respects from European species of the genus, yet appear closely related to them. A still further expansion might allow admission of the fungus here described, but such extreme attenuation of the original concept of the genus *Hydnotrya* seems unjustifiable.

The partitioning of the ascocarp into outward-opening empty chambers possessing hymenium-lined walls, is *Hydnotrya*-like. But in previously known *Hydnotrya* species, these chambers are

either labyrinthine or anomalous in form; the paraphyses are enlarged at the tips and, at external openings, continue into the ascocarp surface as swollen-tipped hyphae which form a superficial velvety "pile"; the asci are clavate with irregularly arranged spores, or cylindrical with spores uniseriate, in either case the spores nearly or completely filling the ascus. In the fungus under discussion, the chambers are large, few, definite in form and not at all labyrinthine; the paraphyses are not swollen-tipped and do not continue into the ascocarp surface as hairs; both paraphyses and asci are conspicuously long and slender; and the small spores are crowded into the distal third or half of the ascus. In addition, the possession of a conspicuous stipe distinguishes the fruiting body of this fungus from any known species of *Hydnotrya*. In the writer's opinion, this combination of dissimilarities provides sufficient basis for the establishment of a new genus related to *Hydnotrya*.

TYPE SPECIES: *Caulocarpa montana*.

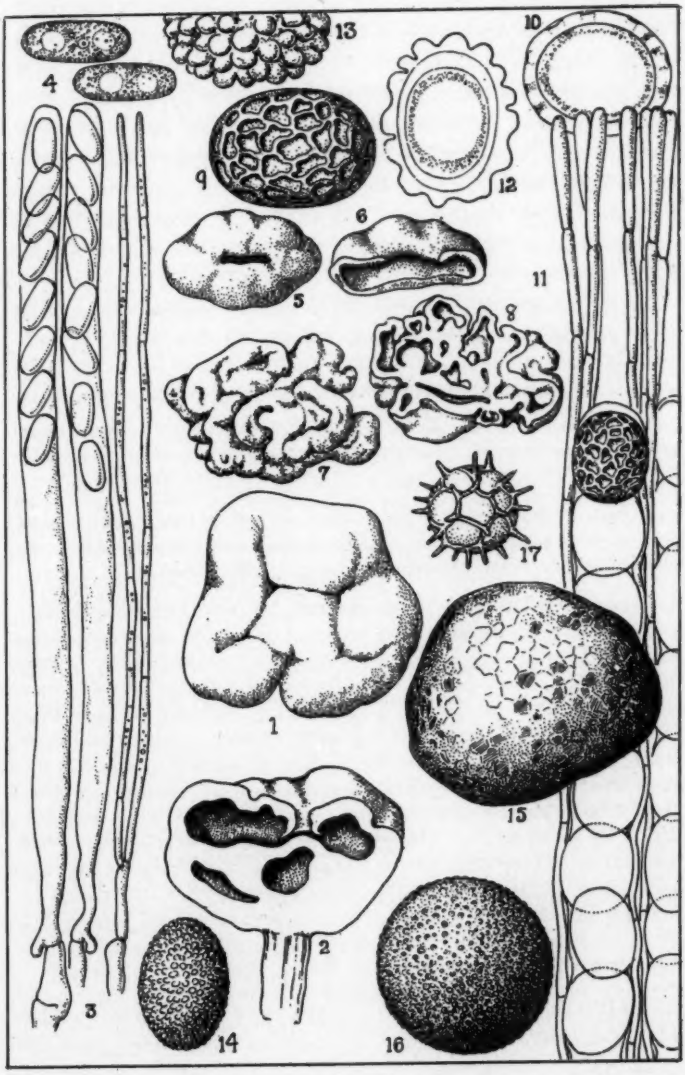
Caulocarpa montana sp. nov. (FIGS. 1–4)

Ascomatibus brunneis, carnosis, globosis aut lente depressis, 2–3.7 cm. diam., lente lobatis, stipitatis; interiore in cava partito, parietibus cavorum hymenio praeditis; textis corticis prosenchymaticis; textis subcorticis laxe hyphalibus; ascis 320 × 10–12 μ; paraphysibus exilibus, longitudine ascis aequis; sporis ellipsoideis, 10–17 × 6–8 μ, pellucidis, levibus, juvenilibus uni aut imperfecte biseriatis, maturis uniseriatis.

Ascocarp Dresden brown (R.), fleshy, nearly globose or slightly flattened, 2–3.7 cm. in diam., nearly regular but with a few thick lobes above, at base narrowed abruptly into a stipe 1 cm. or more long; interior of ascocarp partitioned partially or completely into large empty chambers lined with closely-packed hymenial palisade; cortex compactly prosenchymatous; subcortex and partitions consisting of loosely interwoven conspicuously irregular hyphae; asci 320 × 10–12 μ; paraphyses septate, very slender, acute at apex, equaling asci in length; spores ellipsoid to oblong, with rounded ends, smooth at least at first, 10–17 μ, colorless, generally occupying apical one-third to one-half of ascus.

OREGON: Hat Point (alt. 5500 ft.), margin of Snake River Canyon, Wallowa Co., beneath duff of coniferous grove, A. M. and D. P. Rogers, **type** (*284* H. M. G.).

This fungus, though collected only once, is known from several specimens in various stages of development. Most specimens ob-



FIGS. 1–17.

viously are slightly immature, at which stage the spores are clearly hyaline, smooth, and more or less biseriate in the ascus. As the spores enlarge and assume their characteristic and definite form, they become uniseriate, and their state of maturity is judged from these characters. Whether, however, any of the spores are completely mature, also whether eventually there may be a slight roughening of the surface, cannot be determined with certainty; though there is a faint suggestion of the latter. These studies will be continued when the area in which the fungus was discovered can again be visited.

So far as seen, this is a completely and permanently hypogaeous form, covered an inch or more by coniferous duff.

Hydnotrya variiformis sp. nov. (FIGS. 5–11)

Ascomatibus 0.7–3 cm. diam., argillaceis, subdepressis, regularibus aut penitus lobatis, superficie minute velutinosis; caverna fere simplice aut gleba compactis plicis composita; textis corticis externi pseudoparenchymaticis interne in stratum compacte hyphalem transformantibus; ascis cylindricis aut lente clavatis, 240–280 × 24 μ; paraphysibus ultra ascos 120–140 μ prominentibus; sporis ellipsoideis, brunneis, juvenilibus uni aut rare imperfecte biseriatis, maturis perfecte uniseriatis, minute lacunosis, 24–28 × 32–36 μ.

Ascocarp 0.7–3 cm., cinnamon-buff (R.) to cream-buff (R.), somewhat paler within; form more or less globose to somewhat depressed, minutely velutinous without, exceedingly variable within, from *Peziza*-like with simple cavity and conspicuous opening, to extremely lobed with interior cavity reduced to many small chambers and narrow branching canals among crowded and fused folds, opening obscurely to the surface at several points; cortex pseudoparenchymatous without, changing to "tissue" of intertwined branching hyphae running perpendicular to asci; asci 240–280 × 24 μ, somewhat clavate at first, with developing spores sometimes incompletely biseriate, becoming cylindrical at maturity with spores strictly uniseriate; paraphyses slender, 6 μ thick, extending 120–140 μ beyond asci, tips slightly enlarged; spores 24–28 × 32–36 μ, rounded-oblong or ellipsoid, yellow-brown, minutely and irregularly lacuno-rugose.

CALIFORNIA: Mt. Shasta, Siskiyou Co., W. B. Cooke, **type** (*13371* Cooke; *288* H. M. G.); (*285–287, 289–299, 303–304* H. M. G.).

OREGON: Monument Peak, Linn Co., A. M. Rogers (*321* H. M. G.); Mt. Chintimini (Mary's Peak), Benton Co., Dr. D.

P. Rogers (*356–357* H. M. G.), Beulah and H. M. Gilkey (*281* H. M. G.); Black Rock Lookout, Douglas Co., Daisy Overlander (*355* H. M. G.).

Specimens of this species were collected almost simultaneously, at an altitude of 4000 to 8000 feet, upon widely separated mountain peaks. The spores, in shape, resemble those of *H. ellipsospora* and *H. yukonensis;* but they differ from both and from those of all other known species of *Hydnotrya* in their pitted and wrinkled surface.

The ascocarp exhibits wider variation than has previously been known in any single species of this genus. The simple *Peziza*-like shape found frequently in this species has typical *Gyrocratera* characters of a hollow fruiting body with a single apical opening. The interior, which is lined by hymenium, may be even, or may be complicated by projections from the inner surface. On the other hand, the extremely complicated forms, which also are common in this species, are typically *Hydnotrya*-like, in Fischer's sense (Mykolog. Beitr. **33**: 108–114. 1927), for the hymenium-lined interior is divided, by the fusion of folds, into canals and chambers which may open externally at several points.

This species, by closing the gap between *Gyrocratera* and *Hydnotrya* and identifying them as one, simplifies the explanation of relationship in our American species, several of which have been discovered since Fischer's paper was published.

Hydnotrya yukonensis sp. nov. (FIGS. 12–13)

Ascomatibus 1.5 × 2.5 cm. diam., brunneis, penitus lobatis, superficie minute velutinosis; gleba plicis compactis et irregularibus nonnumquam anastomosantibus et fossas longas labyrinthiformesque et cubicula formantibus composita; textis corticis prosenchymaticis; ascis cylindricis aut lente clavatis, 240–280 × 16–20 μ; paraphysibus ultra ascos 60–100 μ prominentibus; sporis ellipsoideis, juvenilibus uni aut rare imperfecte biseriatis, papillatis, pallide brunneis, 28 × 32–36 μ.

Ascocarp reaching 1.5 × 2.5 cm. in diam., wood-brown (R.), much convoluted, surface minutely velutinous; interior compact, penetrated by canals and chambers; cortex coarsely prosenchymatous, changing within gradually to smaller-celled prosenchyma and to loose branching hyphae, superficial cells forming septate hairs; subhymenial layer frequently penetrated by large branching hyphae, and subhymenial asci occasionally present; asci cylindrical or

slightly clavate at first, 240–280 × 16–20 μ; paraphyses 60–100 μ longer than asci, scarcely or not at all swollen at apex; immature spores hyaline, ellipsoid, somewhat biseriate in ascus; at maturity pale yellow-brown, strictly uniseriate, 28 × 32–36 μ, papillose.

YUKON: Mayo Landing between Whitehorse and Dawson, coll. Catherine Broadfoot, **type** (Central Exp. Farm, Ottawa, also fragment in H. M. G. collection, No. *353*). Collected between 61° and 64° N. lat., at 4500 ft. alt. Submitted by Dr. D. B. O. Savile, Jr. Plant Path., Central Exp. Farm, Ottawa.

In spore development, this species closely resembles *H. carnea, H. Tulasnei,* and *H. cubispora,* in which this process previously has best been known. The spore at first appears hyaline; later the epispore becomes visible as a more or less cubical block in which the hyaline spore proper appears embedded; and eventually the epispore takes its mature shape molded about the cell proper, but with coarse superficial sculpturing. In *H. cubispora,* in which the process is particularly conspicuous, the epispore at maturity (especially of the terminal spore of the ascus) frequently retains permanently its earlier cubical form, the sculpturing sometimes consisting principally of thickened angles without definite papillae. In all three of the above-mentioned species, the original hyaline cell is globose, any elongation such as often is found in the terminal spore of *H. cubispora* being due only to irregularly-distributed thickenings of the epispore.

The definitely ellipsoid spore shape of *H. yukonensis* links this species with the previously known *H. ellipsospora* and with *H. variiformis,* described in this paper. From *H. ellipsospora* it differs, together with other characters, in the much larger spores, very different spore surface, and in the long paraphyses. It has several characters in common with *H. variiformis,* including size and shape of spores, comparative length of asci and paraphyses, and subalpine habitat. However, its papillose spores bear no resemblance, except in size and shape, to the unique lacunose spores of the latter species; and structural differences further separate the two.

GEOPORA GLABRA Gilkey

Since the publication in 1939 of *Geopora glabra* (Tuberales of North America, Ore. State Col. Mono., Bot. 1), further oppor-

tunities for study of this fungus have revealed that the species was established upon immature specimens in which the spores were smooth and hyaline, that mature spores are minutely sculptured, and that definite external openings from the hymenium may be seen in mature ascocarps. The possession of these characters removes the organism from *Geopora* and establishes it as *Hydnotrya*. The spores of all species of *Hydnotrya* are conspicuously hyaline until a very late stage of development, and closely resemble mature spores of *Geopora, Barssia,* and *Pseudobalsamia*.

This species of *Hydnotrya* can be, in size of spores, compared with only one species heretofore described, namely *H. ellipsospora*. It differs from earlier-known specimens of the latter in the complex ascocarp, distinguished by folds and hymenial projections which partition the structure into many canals and chambers. Further, the spores of the type collection of *H. ellipsospora* are typically smaller and somewhat more ellipsoid. However, *H. variiformis,* described in the present paper, demonstrates to the author that extremes in ascocarp configuration can no longer be reckoned among criteria to separate *Hydnotrya* species; and the same may be said for spore shape and size in other genera, and therefore, perhaps, in this.

Spore markings appear identical in *H. ellipsospora* and the organism under discussion whereas shape and size vary considerably in both. Therefore *Geopora glabra* is reduced to synonymy under *Hydnotrya ellipsospora,* with the following emended description:

HYDNOTRYA ELLIPSOSPORA Gilkey emend. (FIG. 14)

Univ. Calif. Pub. Bot. **6**: 307 (1916); Sacc. Syll. Fung. **24**, Sup. Univ. **10** (1928); Fischer, Die natür. Pflanz. Band **5b** (VIII): 23 (1938). *Geopora glabra* Gilkey in Tuberales of North America, Ore. State Col. Monor., Bot. **1**.

Ascomatibus plicis laxis aut compactis compositis; sporis 10–16 × 14–(raro) 19 μ.

Ascocarp from a simple structure consisting of loose folds casually joined, to a compact complicated arrangement of folds and projections separating numerous canals and chambers; spores 10–16 × 14–(rarely) 19 μ.

CALIFORNIA: Pacific Grove, N. L. Gardner and M. B. Nichols, **type** (*316* U. C. Herb.); Saratoga, H. E. Parks (*295* Parks; *18* H. M. G.); Stanford, James McMurphy (*7* H. M. G.); Alma and Guadaloupe, H. E. Parks, **type** of *Geopora glabra* Gilkey (*215* H. M. G.); Frances Simes Hastings Nat. Hist. Reserv., Monterey, J. M. Linsdale (*367, 375, 381, 382, 392* H. M. G.).

OREGON: Corvallis, S. M. Zeller (*253* H. M. G.).

KEY TO AMERICAN SPECIES OF HYDNOTRYA

Spores essentially globose, any elongation occurring in the epispore, only.
- Thickening of epispore giving cubical appearance, especially to terminal spore..... *H. cubispora*
- Thickening of epispore in form of a few coarse rounded protuberances, not giving cubical appearance to spore..... *H. carnea*

Spores ellipsoid.
- Spores not exceeding 20 μ in length, generally much shorter *H. ellipsospora*
- Spores 30 μ or more in length.
  - Spore surface papillose..... *H. yukonensis*
  - Spore surface lacuno-rugose..... *H. variiformis*

Terfezia Longii sp. nov. (FIG. 17)

Ascomatibus subglobosis, ad 3.5 cm. diam., albidis, levibus; textis corticis compactis, crasse pseudoparenchymaticis et prosenchymaticis; ascis multis, subglobosis ad fere cylindricis 60–80 μ; sporis globosis, 20–26 μ, pallidis, reticulatis spinosis.

Ascocarp subglobose, reaching 3.5 cm. in diam., whitish, smooth; cortex consisting principally of coarse pseudoparenchyma and prosenchyma, with occasional irregularly placed large hyphae; sterile "tissue" of gleba looser, principally hyphal and, upon drying, tending to shrink more conspicuously than cortex; walls of all cells thin and delicate; asci globose to somewhat elongate, small, averaging 60–80 μ in length, inconspicuous, not readily separable from glebal "tissue," generally closely packed with spores; spores 20–24 μ (including spines), coarsely alveolate, with generally slender spines at angles of alveoli; number of spines on circumference averaging 15 or fewer.

NEW MEXICO: Near Corono, W. H. Long and D. J. Stouffer *9740*, **type** (*283* H. M. G.).

T. Longii somewhat resembles, in general appearance, *T. spinosa* Hark. which was named in 1899 from specimens collected in Louisiana in 1886 and distributed by Ellis and Everhart under

the name *T. Leonis* Tul. as No. *1782* (Sec. ser., Cent. XVIII). The intriguing possibility of linking the New Mexican material with this species, and heralding a new appearance of this long-lost *Terfezia*, failed after careful comparison revealed constant differences. These are recorded in the description of *T. spinosa* and the *Terfezia* key which follow.

The author takes pleasure in dedicating this new species to its discoverer, Dr. W. H. Long.

TERFEZIA SPINOSA Hark.

Proc. Calif. Acad. Sci., 3d ser. **1**: 277 (1899). Distributed by Ellis and Everhart as *T. Leonis* Tul. (No. *1782*, Cent. XVIII).

Ascocarp subglobose, white or citron, smooth; cortex consisting of both tangled and parallel hyphae, with areas of pseudoparenchyma; sterile "tissue" of gleba principally of closely tangled hyphae as compact as cortex and not inclined to shrink more perceptibly than cortex upon drying; asci many, subglobose to (often) long and narrow, averaging 100–120 μ in length, conspicuous, readily separable from glebal "tissue," spores loosely arranged within; spores 24–28 μ (including spines), spinose, the spines sometimes slender or more often blunt and broadened at base, the bases often anastomosing over surface of spore, sometimes forming an irregular interrupted incomplete alveolation; number of spines on circumference averaging 20 or more.

LOUISIANA: Red River Valley near Natchitoches, E. Forges, **type** (*108*[a] Hk. Col., Stanford; *271* H. M. G.).

TERFEZIA GIGANTEA Imai (FIGS. 15–16)

Proc. Imp. Acad. **IX**: 4, 1933.

In 1939, Dr. L. O. Overholts discovered on a "mossy bank by a stream" in Center County, Pennsylvania, a large hypogaeous fungus which proved to be a *Terfezia*, the third species of this genus taken in America. Upon the single ascocarp found, the following description is based:

Ascocarp 5 × 5.5 cm. in diam., surface nearly smooth but marked off, apparently by cracking of thin superficial layer, into low polygonal areas, these more pronounced upon drying; surface of dried

specimen terra cotta (R.) to burnt umber (R.), probably paler when fresh, with evidence of early tomentum; cortex-like outer sterile area 800 μ or more thick, superficial cells variable, some forming knotted hairs of tomentum; subsurface layer coarsely pseudoparenchymatous, changing gradually to smaller-celled prosenchyma and loose hyphal structure of fertile interiors; asci nearly globose, 100–120 μ in diam.; spores globose, 44–52 μ, aniline yellow (R.), minutely roughened by more or less coalescent granules or by obscure alveolation, epispore 3–4 μ thick.

PENNSYLVANIA: Reitz Gap, Center Co., L. O. Overholts, *22168* (*310* H. M. G.).

With considerable hesitation, this species is identified with *T. gigantea,* named in 1933 by Dr. Sanshi Imai, from specimens in the forests of Hokkaido, Prov. Ishikari, Japan. In general characters it agrees with that species as described, particularly in the very large minutely-sculptured spores. In our specimen, the spores average definitely larger and are distinctly roughened but not "covered with minute spines" as described and figured for the Japanese species. However, such minute sculpturing is interpreted with difficulty, and may be modified by various factors such as degree of spore maturity.

Imai does not mention a tomentum, of which traces are found on the ascocarp here considered; but, being evanescent, it may easily be overlooked. Neither are the low polygonal areas noted, which are conspicuous on our specimen; though these are suggested by Dr. Imai's illustration, and by his description of the ascocarp surface as "rough, with often evident and large crackings."

When comparison with authentic material of *T. giganteum* becomes possible, our specimen may prove sufficiently distinct to merit a new specific epithet; but at present it seems wiser to include it under this large-spored species already established.

KEY TO TERFEZIA SPECIES KNOWN IN AMERICA

Spores 44–52 μ, minutely roughened.....*T. gigantea*
Spores less than 30 μ.
  Spores coarsely and regularly alveolate and spinose, crowded in small inconspicuous asci.....*T. Longii*
  Spores spinose, spines irregularly anastomosing at base; spores loosely arranged in large conspicuous asci.....*T. spinosa*

EXTENSIONS OF RANGE SINCE THE PUBLICATION, IN 1939, OF TUBERALES OF NORTH AMERICA

Barssia oregonensis Gilkey. OREGON: Langdon Lake, Blue Mts., S. M. Zeller (*300* H. M. G.); Roaring River, Linn Co., Lee Powell (*320* H. M. G.).

Genea arenaria Hk. CALIFORNIA: Monterey, Blomquist and Linsdale (*359, 368–9, 374, 384, 386, 394, 399* H. M. G.).

Genea cerebriformis (Hk.) Gilkey. CALIFORNIA: Monterey, Blomquist and Linsdale (*387* H. M. G.). OREGON: Clackamas Co., A. M. and D. P. Rogers (*324–7* H. M. G.).

Genea Gardneri Gilkey. CALIFORNIA: Monterey, Blomquist and Linsdale (*371, 373* H. M. G.).

Genea Harknessii Gilkey. OREGON: Clackamas Co., A. M. Rogers, H. M. Gilkey (*328* H. M. G.).

Genea intermedia Gilkey. CALIFORNIA: Monterey, Blomquist and Linsdale (*360, 385, 389, 400, 401,* H. M. G.).

Geopora Harknessii Fischer. OREGON: Oregon State College Campus, Corvallis, Maxwell Doty (*305* H. M. G.).

Geopora magnata Hk. CALIFORNIA: Pasadena, A. G. Barr (*279* H. M. G.).

Hydnobolites californicus Fischer. CALIFORNIA: Monterey, Blomquist and Linsdale (*377, 379, 383, 393, 395* H. M. G.).

Hydnotrya cubispora (Bessey and Thompson) Gilkey. ALASKA: Ketchikan, Dale Parks (*306* H. M. G.). OREGON: Clatsop Co., E. and F. Smith (*315* H. M. G.); H. M. Gilkey (*316* H. M. G.); Reedsport, H. M. Gilkey (*225* H. M. G.). TENNESSEE: Great Smoky Mts., Dorothy M. Linder (*307* H. M. G.).

Picoa carthusiana Tul. OREGON: Saddle Mt., Clatsop Co., Elizabeth Smith (*319* H. M. G.).

Tuber californicum Hk. CALIFORNIA: Monterey, Blomquist and Linsdale (*388* H. M. G.). OREGON: Clackamas Co., A. M. and D. P. Rogers (*323* H. M. G.).

Tuber candidum Hk. CALIFORNIA: Monterey, Blomquist and Linsdale (*376, 402* H. M. G.).

Tuber dryophilum Tul. MICHIGAN: East Lansing, Forrest C. Strong (*405* H. M. G.).

OREGON STATE COLLEGE,
CORVALLIS, OREGON

EXPLANATION OF FIGURES

FIG. 1. *Caulocarpa montana*, upper view of ascocarp, × 1. FIG. 2. *Caulocarpa montana*, longitudinal section of ascocarp, × 1. FIG. 3. *Caulocarpa montana*, asci and paraphyses, × 400 diam. FIG. 4. *Caulocarpa montana*, spores, × 1000 diam. FIG. 5. *Hydnotrya variiformis*, simple ascocarp, × 1. FIG. 6. *Hydnotrya variiformis*, longitudinal section of simple ascocarp, × 1. FIG. 7. *Hydnotrya variiformis*, convoluted ascocarp, × 1. FIG. 8. *Hydnotrya variiformis*, longitudinal section of convoluted ascocarp, × 1. FIG. 9. *Hydnotrya variiformis*, spore, × 600 diam. FIG. 10. *Hydnotrya variiformis*, longitudinal section of spore, × 600 diam. FIG. 11. *Hydnotrya variiformis*, asci and paraphyses, × 400 diam. FIG. 12. *Hydnotrya yukonensis*, longitudinal section of spore, × 600 diam. FIG. 13. *Hydnotrya yukonensis*, one-half of spore, × 600 diam. FIG. 14. *Hydnotrya ellipsospora*, spore, × 1300 diam. FIG. 15. *Terfezia gigantea*, ascocarp, × ⅔ diam. FIG. 16. *Terfezia gigantea*, spore, × 500 diam. FIG. 17. *Terfezia longii*, spore, × 800 diam.

TAXONOMIC NOTES ON MYXOMYCETES. II

G. W. Martin

Badhamia magna Peck

In his original description of *Dictydium magnum* (Ann. Rep. N. Y. State Mus. **24**: 84. 1872), Peck mentioned the reticulate walls of the sporangia as one of the distinctive characters of the species. Later (Ann. Rep. N. Y. State Mus. **31**: 57. 1879), in transferring the species to *Badhamia,* he emphasized that character, stating that when it is taken into account with the large size and the globose sporangia, the species may readily be separated from forms of *B. utricularis.* A. Lister (Mycetozoa p. 33. **1894**) stated that it is nearly allied to *B. hyalina.* Sturgis (Trans. Conn. Acad. Arts & Sci. **10**: 466. 1900) re-examined Peck's type and re-described and illustrated it, deciding that although closely related to *B. utricularis,* it might be regarded "for the present" as distinct. G. Lister (Mycetozoa ed. **3**, p. 14. 1925) states that it is hardly more than a variety of *B. utricularis.* Macbride (N. A. Slime-Moulds p. 68. **1899**) assigned it provisionally to *B. capsulifera.* Later (N. A. Slime-Moulds ed. **2**, p. 38. 1922), he recognized Peck's species. Macbride & Martin (Myxomycetes p. 31. **1934**) say "distinguished [from *B. utricularis*] by its unclustered, smoother spores and its long, slender, pale stipes." It is also noted that spores from the type collection are oval, umbonate and large and a reproduction of a camera lucida drawing of such a spore is shown on *pl. 2, fig. 26,* accompanied by a drawing from another specimen referred to the species, *fig. 25,* which is not significantly different from the spore of *B. utricularis* shown as *fig. 23* on the same plate. Hagelstein (Mycetozoa p. 20. **1944**) recognizes the species, distinguishing it from *B. utricularis* by the unclustered spores, the more robust sporangia on longer stalks and the darker, more minutely spinulose spores. In his key, he groups *B. utricularis* with the species having clustered spores, and *B. magna* with

those having free spores, but in the text he admits that none of these characters is constant.

Re-examination of an extensive series of collections referred to these two species shows that neither the reticulate character of the peridium nor the long, pale stipes are dependable characters, each merging into the plain peridium and the sessile condition independently of the other. This leaves only the spore characters to consider. Since the spores in the original preparation from the type, preserved in glycerine on a slide, had become badly shrunken, another mount was made from the single cluster which constitutes our portion of the type collection. In this mount, the spores were nearly all spherical, 12 μ in diameter. A number were umbonate, but this character was not as conspicuous as in the previous mount. The only explanation I can suggest for this discrepancy is that the earlier mount was from a portion of a sporangium improperly matured. The spores themselves were no darker, and certainly no smoother than many collections clearly representing *B. utricularis*. Furthermore, the spore clusters supposed to characterize the latter species are by no means always in evidence. We have examples of that species determined by a number of competent students, including A. Lister, in which the spores are wholly free.

Since none of the characters ordinarily supposed to distinguish *B. magna* from *B. utricularis* is constant, I am convinced that Peck's species should be regarded as a synonym of *B. utricularis*.

CRIBRARIA ATROFUSCA Martin & Lovejoy

In the original description of this species (Jour. Wash. Acad. Sci. **22**: 92. 1932), the dark color of the sporangium and spores and the concentric granular rings on the inside of the calyculus are stressed. Hagelstein (Mycetozoa p. 190. **1944**) unites the species with *C. piriformis*. Re-examination of the collections cited in the description and of several additional collections, all from Colorado, confirm the original description in most essentials. The statement that the concentric granular thickenings are deposited on the inside of the cup is, however, misleading. The thickenings take the form of concentric corrugations clearly visible under a good lens on both the outside and the inside of the cup, in marked contrast

with *C. piriformis,* in which the calyculus is distinctly ribbed. It is true that occasional collections of *C. piriformis* are nearly as dark as *C. atrofusca.* Schrader, in his original description, noted the change from blackish purple to brown in maturation. But dark forms of *C. piriformis* show evidence of premature drying, which is not the case in the specimens of *C. atrofusca.* In addition to the dark color and the concentric corrugations on the cup, the spores of *C. atrofusca* are dark reddish brown in mass and grayish brown by transmitted light whereas those of *piriformis* are yellow brown in mass, paler by transmitted light, and slightly smaller.

CRIBRARIA DICTYOSPORA Martin & Lovejoy

As originally described (Jour. Wash. Acad. Sci. **22**: 91. 1932) the distinctive characters of this species were the dark color and the reticulate spores. Hagelstein (Mycetozoa p. 191. **1944**) accepts the species with some reservation, stating categorically that the spores are not reticulate and suggesting that it may be merely a dark phase of *C. piriformis.* Re-examination of the type and cotype shows the reticulation on the spores to be exactly as described in the original publication. The reticulations may be seen under a dry lens; the oil immersion lens brings them out very sharply. Recently a box containing twenty-four undetermined collections of *Cribraria* from Oregon was found among the material put aside by Dr. Macbride for later study. They almost certainly represent specimens sent to him many years ago by Prof. Morton E. Peck. Of the twenty-four, ten are referable to *C. dictyospora.* All ten show the spore reticulations clearly. Two other collections, also from Oregon, which had been determined as other species, also belong here. In view of the abundant material now available, there can be little doubt that *C. dictyospora* is a valid species.

DIDERMA COR-RUBRUM Macbr.

This species was based (N. A. Slime-Moulds ed. **2**, p. 140. 1922) on a single Iowa collection. The entire collection was sent to England for examination and is now in the British Museum. After examining it, G. Lister (Mycetozoa ed. **3**, p. 84. 1925) decided that it was an imperfect development of *D. montanum* and in-

cluded it in the synonymy of that species. Later (Jour. Bot. **75**: 327. 1937), she recognized Macbride's species as valid and reported a collection from Kenya. Hagelstein (Mycetozoa p. 93. **1944**) follows the earlier disposition in the third edition of the Mycetozoa, possibly having overlooked the later reference. Under *D. Lyallii* (p. 100) he records a collection of that species from Kansas. It seems highly probable that this report is based on T. E. Brooks' No. *641,* a portion of which is in the University of Iowa collection. Except for its rather pale, grayish purple columella, this collection agrees very satisfactorily with the original description of *D. cor-rubrum,* and with G. Lister's later comment on the species. It is quite distinct from either *D. montanum* or *D. Lyallii.* If the description of *D. cor-rubrum* is modified to permit such variation in the color of the columella as occurs in other species, the Kansas collection could be included satisfactorily there, and nowhere else.

DIDERMA LYALLII (Massee) Macbr.

Both Lister and Macbride and Martin place this species in *Eudiderma* on the basis of the calcareous outer wall. Lister describes the spores as "dark purplish brown rather coarsely warted, 10–15 μ"; Macbride and Martin say: "dark brown, rough, 14–17 μ." Meylan (Bull. Soc. Bot. Geneva II. **2**: 262. 1910) places the species in the sub-genus *Leangium,* describing the spores as strongly papillate, 13–17 μ in diameter. Receipt of a collection from Mt. Shasta (W. B. Cooke *16670*) with striking spores, characterized by sparsely scattered, long, dark spines, has been the occasion for a re-examination of our material. If the two divisions of *Diderma* are to be maintained, only a narrowly verbal distinction would place *D. Lyallii* in *Eudiderma.* In habit it suggests at sight *Leangium* and even the peridium, although undoubtedly more calcareous and fragile than in most Leangiums, is very like that of the cartilaginous species. None of the spore descriptions is adequate. In those collections which may be regarded as fully developed, the spores are very uniform, the body of the spore being about 15 μ in diameter, rarely under 14 μ or over 16 μ. The spines, which may reach 2 μ in length, if included, would, of course, modify these di-

mensions. In the Shasta collection they are somewhat more sparse than in previous collections studied, but essentially similar to several. Other collections, however, have the surface covered with numerous dark warts, as illustrated in fig. 191 in Macbride and Martin. There may be two species concerned, but it seems more probable that in this, as in other alpine species, the conditions of development may radically affect the surface of the spores as well as the sporangial characters.

The existence of *Lepidoderma*-like plates on the peridium of a Rumanian collection has been noted (Macbride and Martin p. 128). In the Shasta collection, similar plates, distinctly crystalline, occur on the substratum, presumably secreted by the hypothallus.

DIDYMIUM SERPULA Fries

Didymium complanatum (Batsch) Rost. (Mon. p. 151. **1874**) is based on *Lycoperdon complanatum* Batsch (Elench. Fung. Cont. **1**: 251, *pl. 29, fig. a–c.* 1786). Rostafinski cites *D. Serpula* Fries (Syst. Myc. **3**: 126. 1829) as a synonym. Rostafinski's combination is, however, a later homonym of *D. complanatum* Schrad. (Nov. Gen. Pl. p. 24, *pl. 5, fig. 5.* **1797**) and *D. complanatum* Fuckel (Symb. Myc. **1**: 341. 1870). Neither Schrader's description nor his figure makes it possible to be sure to what his name applies. Rostafinski cites it as a synonym of his *D. confluens* which in its turn is generally regarded as a synonym of *D. crustaceum* Fries, but G. Lister (Mycetozoa ed. **2**, p. 129. 1911) cites it as a doubtful synonym of *D. melanospermum* (Pers.) Macbr. There seems to be no doubt that Fuckel's name is a synonym of *Diderma radiatum* (L.) Morgan. DeBary (Mycetozoen, *pl. 2, fig. 9–16.* **1864**) refers to *D. Serpula* Fries and his figure *15* leaves no doubt as to the species he was studying. Rostafinski himself (Mon. App. p. 21. 1876) substituted *D. Serpula* Fries for *D. complanatum* Rost. and cites his illustrations, *pl. 9, fig. 166, 180,* as representing it. A. Lister (Mycetozoa p. 96. 1899) used the epithet *Serpula,* but G. Lister (Mycetozoa ed. **2**, p. 127. 1911) reverts to *complanatum* on the ground that "no writers before Rostafinski make any mention of the characteristic vesicles of the capillitium," overlooking deBary's clear description.

Certainly *D. complanatum* Rost. is not valid. Rather than coin a new name, it seems desirable to accept the species of Fries in the sense in which DeBary interpreted it, and Rostafinski, on maturer thought, applied it.

ENTERIDIUM MINUTUM Sturgis

Of the five currently recognized species of *Enteridium*, the common *E. Rozeanum* is readily recognized by its ferruginous colors and its incompletely reticulate spores. *E. yabeanum*, known only from Japan, is darker, but is also said to have completely free spores which are uniformly warted and smaller than those of any other species. The remaining three species are reported as having their spores borne habitually in clusters, or rarely free. Of these, only *E. olivaceum* may be said to be satisfactorily established. *E. liceoides* was originally described by A. Lister (Jour. Bot. **34**: 211. 1896) as a variety of *olivaceum* differing from the species only in its small size and plasmodiocarpous habit. It was later raised to specific rank by G. Lister (Guide Brit. Mycet. ed. **4**, p. 48. 1919). The last-named reference is not available to me, but neither in the original description of the variety nor in the discussion in the latest edition of the Lister monograph (ed. **3**, p. 194. 1925) is there convincing evidence that it is more than a small, dark, growth-form of *E. olivaceum* with depauperate pseudocapillitium. *E. minutum* Sturgis (Mycologia **9**: 329. 1917) is described as very small, the aethalia 1.5–2 mm. in diameter, with a pale yellow wall and with the spores in small clusters of two or three and yellow in mass. Sturgis described it as new with much hesitation and only after consultation with Miss Lister, but nevertheless in the third edition of the Mycetozoa the latter remarks that it is doubtful if *E. minutum* is more than a small form of *E. olivaceum*. In the 1896 paper cited, A. Lister had commented on the occurrence of *E. olivaceum* with free spores and in both the key and the description of the latter species in the Mycetozoa it is stated that the spores are sometimes free. In Macbride and Martin (Myxomycetes p. 236. **1934**) the distinction between free and clustered spores is given as the first character in the key to *Enteridium* to separate the two groups of species, and no allowance

is made for free spores in *E. olivaceum*. This was in accordance with the material available for study at the time the key was written. Since then, much new material has come to hand and it appears that the description of that species must be modified. Of particular interest are several collections from Mt. Shasta, California, at an altitude of 8000 feet, communicated by Mr. W. B. Cooke. His No. *10263* consists of numerous fructifications, most of them rather small, varying from typical aethalia of the *olivaceum* type to plasmodiocarps of the *liceoides* type and small pulvinate structures of the *minutum* type. The spores are entirely free and vary from globose and 13–14 μ in diameter to oval and about 15 $\times$ 11 μ. Another specimen from Mt. Rainier, Washington, collected at 7000 feet by Dr. H. C. Greene, consists of a single broad, flat aethalium 9 cm. long and 1–2 cm. in width with the spores in small, loose clusters, mostly of twos or threes, with spines on the exposed surfaces only and 14–15 μ in diameter. It differs from what has been regarded as typical *E. olivaceum* only in the large aethalium and the large spores in small clusters. I conclude, therefore, that *E. liceoides* is a definite synonym of *E. olivaceum* and that *E. minutum* is in all probability nothing more than a small form of the same species. *E. Rozeanum* is, of course, quite distinct and *E. yabeanum,* so far as can be judged from the description, equally so.

LYCOGALA EXIGUUM Morgan

The characters stressed by Morgan (Jour. Cin. Soc. Nat. Hist. **15**: 134. 1893) in establishing this species were the small size, the dark color, the rather slender threads of the pseudocapillitium and the reticulate surface pattern made by the dark scales on the cortex. Of several specimens collected or determined by Morgan now in the University of Iowa collection, one, collected in Ohio in 1893, is in all probability part of the type. The scales of this specimen, when examined under the microscope, show the characteristic tessellate appearance which is the distinctive basis on which *L. epidendrum* var. *tessellatum* Lister (*in* Penzig, Myx. Buit. p. 77. **1898**) was established. The spores are 5.5–6 μ in diameter, marked with faint warts and lines forming a very incomplete reticulate pattern on the surface, quite different from those of typical *L.*

epidendrum in which the spores are larger and the reticulation is complete or nearly so and is visible under a dry lens as the hyaline rim characteristic of reticulate spores in general. The tessellate character of the scales shows a wide range of variation and is not always evident, but the small, dark fructifications with dark, scale-like warts, slender pseudocapillitium and the characteristic spores justify recognition of *L. exiguum* as a valid species. *L. epidendrum* var. *tessellatum* Lister is a synonym. Of the specimens in the University of Iowa collection determined as *L. epidendrum* var. *exiguum*, a few are merely small, dark fruitings of *L. epidendrum*. The majority are *L. exiguum*. All specimens sent as *L. epidendrum* var. *tessellatum*, including Hagelstein's No. *13332*, also represent *L. exiguum*.

Oligonema Schweinitzii (Berk.) comb. nov.

Oligonema nitens (Lib.) Rost. is based on *Trichia nitens* Lib. (Pl. Crypt. Ard. Fasc. **3**: 277. 1834). *T. nitens* Lib. is, however, a homonym of *T. nitens* Pers. (Obs. Myc. **1**: 62. 1796). Persoon cites *Lycoperdon favogineum* Batsch 1786 and *Stemonitis favoginea* Gmel. 1789 as synonyms of his species. All three names are universally recognized as synonyms of *Trichia favoginea* Pers. 1794, although this combination is not mentioned in the *Observationes*. The specific epithet *nitens* has been universally accepted for the *Oligonema* and is eminently appropriate, but unless some provision is made for the conservation of specific epithets, the disadvantages of which would, in my opinion, far outweigh its occasional convenience, the combination *O. nitens* is invalid and must be replaced by a combination employing the next available specific name. This appears to be provided by *Physarum Schweinitzii* Berk. (Grevillea **2**: 66. 1873). Berkeley's name was given to a specimen which had been determined by Schweinitz as *Polyangium vitellinum* Link, now regarded as one of the Myxobacteriales. Whatever that name refers to, it does not come under consideration in this connection. Lister (Mycetozoa p. 174. **1894**) states that *"Physarum Schweinitzii* Berk. [is] typical *O. nitens*." The new combination here proposed is, therefore, in accord with the current rules of nomenclature.

PHYSARUM CONFERTUM Macbr.

No type is designated in the original description (N. A. Slime-Moulds ed. **2**, p. 64. 1922). In the University of Iowa herbarium, there are several specimens of this species which were studied by Macbride. Three small boxes, apparently all parts of the same collection, and labelled in Macbride's hand *Physarum confertum,* contain perhaps the most representative material. One is marked "N. C." All are on dead leaves of some ericaceous plant. The best of these is designated as the type, and the type locality is North Carolina.

Physarum stellatum (Massee) comb. nov.

According to A. Lister (Mycetozoa p. 45. **1894**), the type specimen of *Lepidoderma stellatum* Massee (Grevillea **17**: 60. 1889) is "a fine specimen of *Physarum compactum.*" This comment is repeated by G. Lister in the second edition of the monograph. In the third edition (p. 32) she adopts the name *P. columbinum* (Rost.) Sturgis for the species, noting that the type specimen of *Lepidoderma stellatum* Massee is "a fine specimen" of the species. But *P. compactum* A. Lister and *P. columbinum* Sturgis are both later homonyms, the one of *P. compactum* Ehrenb. 1818, the other of *P. columbinum* Pers. 1795. Noting this, Macbride (N. A. Slime-Moulds ed. **2**, p. 72. 1922) proposed the new name *Physarum Wingatense* for the species. This name was adopted by Macbride and Martin (Myxomycetes p. 69. **1934**) and by Hagelstein (Mycetozoa p. 40. **1944**). In view of the availability of Massee's earlier specific epithet, Macbride's name is untenable.

Tubifera microsperma (Berk. & Curt.) comb. nov.

Tubifera stipitata (Berk. & Rav.) Macbr. (N. A. Slime-Moulds p. 157. 1899) is based on *Licea stipitata* Berk. & Rav. *ex* Berk. & Curt. (Proc. Am. Acad. Arts. & Sci. **4**: 125. 1859), which, however, is a later homonym of *Licea stipitata* DC. (Fl. Fr. **6**: 101. 1815) which, in turn, is a synonym of *Didymium squamulosum* (Alb. & Schw.) Fries. *Licea microsperma* Berk. & Curt. (Grevillea **2**: 68. 1873) is cited by Massee (Mon. p. 40. **1892**) as a synonym of *Tubulina cylindrica* Rost., *i.e., Tubifera ferru-*

ginosa (Batsch) Gmel., "from exam. of type" and this is followed by G. Lister in the second edition of the Mycetozoa (**1911**, p. 192). In the third edition, however (**1925**, p. 188), she enters it as a synonym of *T. stipitata,* without comment. It seems reasonable to assume that so careful a student would not have made the change without adequate reason, particularly as the type collection was accessible to her. The inadequate and unsatisfactory original description, so far as it goes, suggests that it refers to the small-spored species. Certainly, *Tubifera stipitata* is invalid. On the basis of Lister's synonymy, *Licea microsperma* furnishes the earliest valid specific epithet which may be applied to the species.

STATE UNIVERSITY OF IOWA,
IOWA CITY

STUDIES ON SOME FUNGI FROM NORTHWESTERN WYOMING.[1] IV. MISCELLANEOUS

LEWIS E. WEHMEYER

(WITH 2 FIGURES)

The previous papers of this series (**19**) were concerned with the Pyrenomycetes and Fungi Imperfecti which were collected by the writer during the summer of 1940. A general account of the area and of specific localities in which these collections were obtained will be found in the first paper. The present paper lists the fungi of the groups not previously treated, chiefly the Uredinales and Discomycetes.

The rusts are abundant on a wide variety of hosts in this region. Most of the species collected have been previously reported from the Northwest. Many fleshy fungi and Discomycetes also occur in this area but their occurrence is very sporadic, depending upon the local and occasional rains, or upon other sources of moisture as springs, moist creek beds and the like. Most of the fungi of this type were collected upon two occasions, in Indian Paint Brush Canyon in the Teton National Park and at the Hoback Canyon Forest Camp, as can be seen from the localities cited. Both of these collecting trips were made into these localities a few days after one of the heavy local showers of late summer. Dr. A. H. Smith has kindly determined the Agaricaceae.

EXOASCACEAE

TAPHRINA ALPINA Johans.

Causing a profusely branching "witches-broom" growth, the leaves of which turn yellowish to brown. Hymenium on the underside of the leaf but showing no superficial indication of its presence, even under a lens. Ascogenous cells thick-walled, hyaline, 10–18 × 9–10 μ, forming a network just beneath the epidermis, or

[1] Papers from the Department of Botany of the University of Michigan No. 844.

occasionally rupturing this tissue. Asci mostly hypophyllous, small, 21–27 × 8.5–9.5 μ. Ascospores globose, 3.5–5 μ in diameter.

Camp Davis: on *Betula glandulosa* Michx., July (*1259*).

This material was sent to W. W. Ray for examination and the following quotation from his conclusions (*in litt.*) agrees in all respects with those reached by the writer: "In reading over the description of *T. alpina* and *T. nana,* there is little to separate them and it may well be they are really the same. . . . On the basis of the position of the majority of the asci (hypophyllous) and the frequent occurrence of insertion of the basal cells between the epidermal cells, I am inclined to call the collection *T. alpina.*"

DISCOMYCETES

HETEROSPHAERIA LINARIAE (Rab.) Rehm

Glory Mt.: on *Linaria vulgaris* Mill., June 20 (*1023*).

The spores of this collection are pyriform to clavate, one celled, hyaline and 10(–12) × 3.5–5 μ. They may be somewhat immature, but are slightly smaller than the spore measurements given for *H. Linariae* (9–14 × 3–4 μ), and are more nearly like those of *H. Patella* var. *Lojkae* Rehm, reported from the high Alps, with small clavate spores (9–12 × 2.5–3 μ). The small apothecia (500–800 μ in diameter) and the occurrence on *Linaria,* on the other hand, suggest this species.

The conidial stage of species of *Heterosphaeria* has been reported as consisting of lunate, fusoid, often appendaged conidia, borne in pycnidia similar in appearance to the young enclosed apothecium. Tulasne (**17**, p. 176) and others report that conidia may even be mixed in with the ascus hymenium. Brefeld (**2, 10**: 182–87) reports such lunate conidia and also ellipsoidal "microconidia" from ascospore cultures of *Heterosphaeria* spp. These pycnidial stages have been referred to the genus *Heteropatella,* which Fuckel (**7**) described as a Discomycete without ascospores. His *H. lacera,* with conidia one-celled, curved, appendaged, and with an overall length of 64–72 μ, is given as the conidial stage of *Heterosphaeria Linariae.* The conidia of *H. Patella* are given by Tulasne as 25–30 × 3.5 μ and one-celled but becoming septate upon germination.

As previously pointed out (**19**, II) *Heteropatella umbilicata* (Pers.) Jaap is very common on many hosts at high altitudes in Wyoming. In no case, however, was the ascus stage of a *Heterosphaeria* found on any of these collections, and no *Heteropatella* pycnidia or conidia were found associated with this collection of *Heterosphaeria Linariae*. Rehm (**14**) states that *Heterosphaeria Patella* is seldom found in the ascus stage, although the conidial stage is common. It is possible that *Heteropatella umbilicata,* which has conidia more like those of *Heterosphaeria Patella,* is the conidial stage of this or a similar species.

Karschia adnata Kanouse sp. nov.* (FIG. 1–2)

Apothecia dispersa, superficialia, sessilia, late adfixa, 250–750 μ diametro, convexa, glabra vel modice aspera, atra, marginata, si umida mollia, cerea;

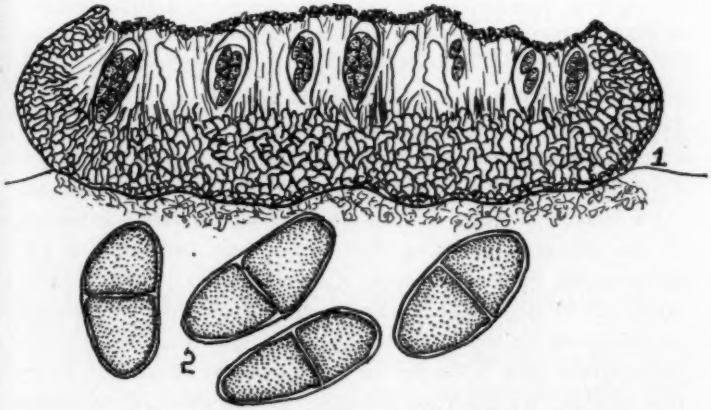


FIG. 1. Section of apothecium of *Karschia adnata.*
FIG. 2. Ascospores of *Karschia adnata.*

superficie inferiore grisei-brunnea, margine concoloria. Hypothecium tenue, pallidum, pseudoparenchymatosum; excipulo simili sed cellulis majoribus, pallide brunneis. Asci crasse clavati, 6- vel 8-spori, 65–80 μ longi, 18–20 (25) μ crassi. Sporae crasse ovoideae, variae, 18–22 (24) μ longae, 8–12 μ crassae, aurei-brunneae, uniseptatae, apice rotundatae; cellulis ambobus guttulatis, saepe inaequalibus. Paraphyses numerosi, ramosi, apicibus clavatis vel subglobosis, atro-brunneis, supra ascos producti et epithecium brunneum densum formans. Hymenium cum iodo nitide caeruleum.

* The writer is indebted to Dr. B. B. Kanouse for the description and discussion of this species.

Specimen typicum ex ligno coniferarum, in Hoback Canyon, Jackson, Wyoming, 16 Julii, 1940, legit L. E. Wehmeyer, sub numero *1154;* in Herb. Univ. Mich. conservatum.

Apothecia sessile, superficial, scattered or gregarious, broadly attached, convex when moist, 0.25–0.75 mm. in diameter, smooth to slightly roughened, soft-waxy when moist, black, marginate; margin grayish-tan, concolorous with the under surface, inconspicuous when wet; hypothecium thin, colorless, hyphal cells compacted into pseudoparenchymatic tissue, excipulum scarcely distinguishable from the hypothecium, cells slightly larger and colored faintly brown; asci broadly clavate, 65–80 × 18–20 (25) μ, 6–8 spored; spores broadly ovate-oblong, variable, frequently slightly constricted at the septum, golden brown, two-celled, cells frequently unequal in size, each cell containing an oil globule, the ends rounded or sometimes provided with a minute point, 18–22 (24) × 8–12 μ; paraphyses numerous, branched above one or more times, the apical cells clavate to subspherical, the upper portions colored dark brown, extending beyond the asci and forming a dense brown epithecium; the hymenium, excepting the spores, turns a brilliant blue in iodine.

On weathered coniferous wood, Hoback Canyon, Wyoming, July 17, 1940. L. E. Wehmeyer, No. *1154* (**type**). Additional collection, Hoback Canyon, July 16, L. E. Wehmeyer, No. *1148*. Type deposited in the Herbarium of the University of Michigan.

Of the many species of *Karschia* described on woody substrata, but few are reported lacking algal cells in their thalli. Butler (3) discusses but two such species, *K. lignyota* (Fr.) Sacc. and *K. stygia* (B. & C.) Massee. Our fungus differs from *K. lignyota,* on coniferous substrata, in having larger spores and lacking the yellow-green color in the hymenium, mentioned by Butler (3) for that species. *K. stygia* has not been reported on coniferous wood and differs from *K. adnata* in the narrow central attachment and red-brown hypothecial color of the apothecium and the conspicuous hexagonal cells in the excipulum. Velenovsky (18) described two species, *K. juniperi* and *K. microscopica,* growing on coniferous wood but the spores of both of these are smaller than those of *K. adnata. K. Sabinae* Rehm and *K. occidentalis* Earle, also reported on conifer wood, have been removed to other genera by Miss Butler (3).

A few groups of a one-celled alga were found in the hypothecia of some of the cups. There was no direct connection between the

algae and the fungous hyphae, such as is seen in a lichen. They are believed to be merely inclusions and were seen more frequently in immature apothecia.

NAEVIA EPILOBII Karst.

South of Teton Pass: on *Epilobium angustifolium* L., July 11 (*1116b*).

The scattered, brownish-yellow apothecia are associated with those of *Pyrenopeziza compressula* on the same stems. The spores are immature, ellipsoid, one-celled, hyaline, and measure 14–19 × 6–7 μ. Nannfeldt (**11**, p. 191) says that this species belongs in his genus *Laetinaevia*.

PHRAGMONAEVIA EMERGENS (Karst.) Rehm

Elk Refuge, Jackson, Wyo., on *Juncus filiformis* L., July 1 (*1072c*).

Rehm (**14**) gives the spores of this species as narrow-clavate, pointed at one end, slightly curved, two- to four-celled and 12–21 × 1.5–2 μ. The spores of this collection are somewhat immature, fusoid, two-celled and 14–18 × 2.5–3.5 μ. Otherwise there is close agreement. Whether this difference in the spores is due to immaturity or is constant in this region can be determined only by the study of additional collections.

PYRENOPEZIZA COMPRESSULA Rehm

South of Teton Pass: on *Epilobium angustifolium* L., July 11 (*1116a*).

The apothecia appear as scattered black discs which, when young, are surrounded by a white halo caused by the raised blister of epidermis. The spores are one-celled, hyaline, slightly curved, cylindric to fusoid and 9–11.5 × 1.5–2 μ.

This collection agrees very well with the description of the above species, except for the gray-blue hymenium which was not seen in these young apothecia.

PYRENOPEZIZA CALIFORNICA Sacc.

Camp Davis: on *Linum Lewisii* Pursh, June 24 (*1047*).

This collection has slightly smaller apothecia (150–250 μ), narrower spores (12–13 × 2–2.5 μ) and broader asci (40–53 × 7–9 μ)

than those originally given for this species, but these differences do not seem to be of specific significance.

HELVELLA CRISPA Fr.

Teton National Park: on damp mossy bank, Indian Paint Brush Canyon, July 30 (*1230*).

A very small specimen (1.5 cm. tall) of this species.

HUMARINA PURPUREA Seav.

Hoback Canyon: on mossy soil, Forest Camp, July 22 (*1222*).

The spores are hyaline to pale brown, finally slightly verrucose, with a large central guttula and 21–23 × 12–13 μ, which is somewhat larger than the measurements given by Seaver (13–20 × 8–10 μ).

LAMPROSPORA HAEMASTIGMA (Hedw.), Seav.

Hoback–Snake River Junction: on damp soil, July 17 (*1151*).

The spores (13–16 μ diam.) are somewhat smaller than given by Seaver (20 μ).

MORCHELLA ANGUSTICEPS Pk.

Teton National Park: on soil, moist creek bed, Cascade Canyon, June 27 (*1227*).

PATELLA SETOSA (Nees) Seav.

Hoback–Snake River Junction: on mossy decayed wood, July 17 (*1150*).

PEZIZA FIMETI (Fck.) Seav.

Hoback Forest Camp: on horse dung, July 22 (*1231*).

This species differs from *P. sylvestris* only in its habitat on dung.

PEZIZA REPANDA Pers.

Teton National Park: on damp soil, Indian Paint Brush Canyon, July 20 (*1225*).

PEZIZA SYLVESTRIS (Boud.) Sacc. & Trott.

Hoback Canyon: on moist humus, poplar thicket, July 3 (*1228*).

PSEUDOPLECTANIA NIGRELLA (Fr.) Fck.

Teton National Park: on damp soil, Indian Paint Brush Canyon, July 30 (*1226*).

PYRENOMYCETES

ERYSIPHE POLYGONI DC.

Hoback Canyon: on *Polygonum aviculare* L., Aug. 6 (*1203*).

SPHAEROTHECA PANNOSA (Wallr.) Lév.

South of Teton Pass: on *Geranium Parryi* (Engelm.) Heller, July 11 (*1270*).

UREDINALES

CHRYSOMYXA ARCTOSTAPHYLI Diet. Camp Davis: on *Arctostaphylos Uva-ursi* (L.) Spreng. (III), June 26 (*1057*).

COLEOSPORIUM SOLIDAGINIS (Schw.) Thuem. Camp Davis: on *Aster* sp. (III), July 4 (*1083*) and *Pinus contorta* Dougl. (I), July 5 (*1081*).

CRONARTIUM COMMANDRAE Pk. Camp Davis: on *Commandra pallida* A. DC. (II), June 18 (*1014*) and July 18 (*1156*) and (II & III), Aug. 2 (*1250*).

CUMMINSIELLA SANGUINEA (Pk.) Arth. Hoback Canyon: on *Mahonia aquifolium* (Pursh) Nutt. (O & I), July 3 (*1263*) and (II & III), June 25 (*1054*).

GYMNOSPORANGIUM JUVENESCENS Kern. Camp Davis: on *Amelanchier elliptica* A. Nels. (O & I), Aug. 6 (*1202*).

HYALOPSORA POLYPODII (Pers.) Magn. Hoback Canyon: on *Filix fragilis* (L.) Underw. (II), Red Creek, July 29 (*1182*).

MELAMPSORA ABIETI-CAPRAEARUM Tubeuf. Teton National Park: on *Salix* spp. (II), Cascade Canyon, June 27 (*1060*). Indian Paint Brush Canyon, July 30 (*1189*) and Phelps Lake, Aug. 5 (*1247*).

The measurements of the urediospores of these three collections are, respectively, 14–15 × 18–20; 12.5–14 × 15–18 and 12–16 × 14–20 μ. The thickness of the urediospore walls is 1.5–2.5; 1.5–1.7 and 2–3 μ. There is little to choose here between this species and *M. Ribesii-purpureae*. The thickness of the walls of the last collection suggests the latter species.

MELAMPSORA ALBERTENSIS Arth. Camp Davis: on *Pseudotsuga mucronata* (Raf.) Sudw. (I), June 25 (*1052*). Hoback Canyon: on *Pseudotsuga mucronata* (I), Forest Camp, July 3 (*1264*). Teton National Park: on *Populus tremuloides* Michx. (II), Indian Paint Brush Canyon, July 30 (*1190*) and Phelps Lake, Aug. 5 (*1248*).

MELAMPSORA BIGELOWII Thuem. Camp Davis: on *Salix* sp. (II), Aug. 2 (*1251*).

MELAMPSORA OCCIDENTALIS Jacks. Teton National Park: on *Populus angustifolia* James (II), Phelps Lake, Aug. 5 (*1207*). The urediospores of this collection were elongate ellipsoid, 30–40 × 16–21.5 μ, and their walls were 1.5–3.5 μ in thickness, or up to 5.5 μ at the thickest region.

MELAMPSORA LINI (Pers.) Lév. Camp Davis: on *Linum Lewisii* Pursh (II), June 24 (*1042*).

MELAMPSORELLA CERASTII (Pers.) Schroet. Granite Creek Hot Springs: on *Picea Engelmanni* (Parry) Englem. (O), June 23 (*1037*) and *Abies lasiocarpa* (Hook.) Nutt. (I), Aug. 1 (*1195*).

PHRAGMIDIUM IVESIAE Syd. Camp Davis: on *Potentilla viridescens* Rydb. (II & III), June 25 (*1049*) and *P. pectinisecta* Rydb. (II & III), June 23 (*1050*).

PHRAGMIDIUM MONTIVAGUM Arth. Camp Davis: on *Rosa* sp. (III), July 18 (*1157*). Dr. G. B. Cummins, to whom material of this collection was sent, comments (*in litt.*): "No. *1157* is probably *P. montivagum* but might be *P. Rosae-arkansanae*, the teliospores and pedicels agree better with the latter but the species is not a mountain species."

PHRAGMIDIUM OCCIDENTALE Arth. Hoback Canyon: Red Creek, on *Rubus parviflorus* Nutt. (I), July 18 (*1268*) and (I & III) July 29 (*1178*). Teton National Park: on *Rubus parviflorus* (I), Jenny Lake, June 27 (*1058*) and (III), Phelps Lake, Aug. 5 (*1249*).

PHRAGMIDIUM ROSAE-ACICULARIS Liro. Hoback Canyon: on *Rosa* sp. (III), Red Creek, July 29 (*1179*), *fide* G. B. Cummins.

PHRAGMIDIUM RUBI-IDAEI (DC.) Karst. Teton National Park: on *Rubus strigosus* Michx. (I), Jenny Lake, June 27 (*1059*).

PUCCINIA ABSINTHII (Hedw. f.) DC. Camp Davis: on *Artemisia tridentata* Nutt. (II) on leaves, (III) on stems, July 13 (*1137*) and *A. cana* Pursh (III), Aug. 3 (*1200*). Hoback Canyon; on *A. tridentata* (II), July 16 (*1146*).

PUCCINIA ASTERIS Duby. Granite Creek Canyon: on *Aster* sp. (III), Aug. 1 (*1196*), *fide* E. B. Mains.

PUCCINIA ATROFUSCA (Dudl. & Thomp. Holw. Teton National Park: on *Artemisia ludoviciana* Nutt. (I), Death Canyon, Aug. 5 (*1205*).

PUCCINIA BALSAMORRHIZAE Peck. Camp Davis: on *Balsamorrhiza sagittata* (Pursh) Nutt. (II & III), July 1 (*1069*).

PUCCINIA CALOCHORTI Peck. Camp Davis: on *Calochortus Nuttallii* T. & G. (III), June 22 (*1039*).

PUCCINIA CARICIS var. URTICATA (Kern) Arth. Camp Davis: on *Urtica* sp. (I), June 22 (*1040*).

PUCCINIA CORONATA Cda. Camp Davis: on *Shepherdia canadensis* (L.) Nutt. (I), June 17 (*1018*).

PUCCINIA CRANDALLII Pam. & Hume. Camp Davis: on *Symphoricarpos pauciflorus* (Robbins) Britt. (I), June 17 (*1019*) and July (*1261*). Hoback Canyon: on *S. pauciflorus* (I), July 29 (*1267*).

PUCCINIA EXTENSICOLA var. HIERACIATA (Schw.) Arth. Camp Davis: on *Agoseris glauca* (Nutt.) Greene (I), June 17 (*1007*).

PUCCINIA EXTENSICOLA var. VALERIANAE Arth. Elk Refuge: on *Valeriana edulis* Nutt. (I), July 1 (*1070*). This material was examined by E. B. Mains and placed here rather than in *P. commutata*, because of the lack of uredia on infections with well advanced aecial pustules.

PUCCINIA GRINDELIAE Peck. Hoback Canyon: on *Erigeron salsuginosus* Gray (III), July 3 (*1077*) and *Aster Engelmannii* D.C.

Eat. (III), July 16 (*1147*). Teton National Park: on *Chrysopsis fulcrata* Greene (III), Aug. 5, Death Canyon (*1206*).

PUCCINIA HALENIAE Arth. & Holw. Skyline Trail: on *Gentiana calycosa* Griseb. (III), Overlook, Aug. 5 (*1204*).

PUCCINIA HEUCHERAE (Schw.) Diet. Hoback Canyon: on *Saxifraga arguta* Don (III), Red Creek, July 29 (*1183*).

PUCCINIA HIERACII (Schum.) Mart. Camp Davis: on *Hieracium* sp. (I), June 17 (*1005*); *Crepis acuminata* Nutt. (II & III), June 28 (*1038*) and *Taraxacum* sp. (II), July 29 (*1181*).

PUCCINIA HOLBOELLII (Hornem.) Rostr. Togwotee Pass: *Arabis canescens* Nutt. (III), July 8 (*1102*), elev. 11,000 ft.

PURRINIA JONESII var. TYPICA Arth. Teton Pass Road: on *Umbellifer* (*Cogswellia* sp.?) (I), June 20 (*1021*).

PUCCINIA MONOICA (Pk.) Arth. Togwotee Pass: *Smelowskia americana* Rydb. (I), July 8 (*1098*), elev. 10,500 ft.

PUCCINIA ONOPORDI Syd. Camp Davis: on *Onopordon Acanthium* L. (II), Aug. 1 (*1068*). This species is reported, in Arthur's Manual (1), only from Nova Scotia, and does not seem to have been previously reported from the West.

PUCCINIA PALMERI Diet. & Holw. Camp Davis: on *Pentstemon procerus* Dougl. (I), June 18 (*1013*).

PUCCINIA RUBIGO-VERA var. AGROPYRI (Erikss.) Arth. Camp Davis: on *Delphinium Brownii* Rydb. (I), June 22 (*1041*); *Thalictrum occidentale* Gray (I), June 17 (*1008*) and *Thalictrum* sp. (I), June 26 (*1266*). Cream Puff Mt.: on *Aquilegia coerulea* James (I), July 5 (*1087*). Hoback Canyon: on *Delphinium Brownii* (I), Granite Creek, July 29 (*1262*). South of Teton Pass: on *Clematis Douglassii* Hook. (I), July 11 (*1123*).

PUCCINIA RUBIGO-VERA var. AGROPYRINA (Erikss.) Arth. Camp Davis: on *Anemone cylindrica* Gray (I), June 18 (*1012*) and *A. globosa* Nutt. (I), June 22 (*1265*).

PUCCINIA RUBIGO-VERA var. APOCRYPTA (Ell. & Tr.) Arth. Hoback Canyon: on *Phacelia leucophylla* Torr. (I), June 25 (*1053*);

P. sericea (Graham) A. Gray (I), June 25 (*1051*). Teton Pass Road: on *Hydrophyllum capitatum* Dougl. (I), June 20 (*1034*).

PUCCINIA VAGANS (DC.) Arth. var. EPILOBII-TETRAGONI DC. Hoback Canyon: on *Epilobium* sp. (II & III), Aug. (*1252*), *fide* E. B. Mains.

PUCCINIASTRUM GOEPPERTIANUM (Kühn) Kleb. Teton National Park: on *Vaccinium scoparium* Leib. (III), Skyline Trail, July 24 (*1165*) and *V. membranaceum* Dougl. (III), Indian Paint Brush Canyon, July 30 (*1256*). Collections of the aecial stage on *Abies lasiocarpa* (Hook.) Nutt. from Cascade Canyon, Teton National Park (*1062*) and Hoback Forest Camp (*1260*) appear to be this species, but might be *P. pustulatum*.

PUCCINIASTRUM PUSTULATUM (Pers.) Diet. Hoback Canyon: on *Epilobium angustifolium* L. (II), July 17 (*1149*).

UROMYCES GLYCYRRHIZAE (Rab.) Magn. Snake River Canyon: on *Glycyrrhiza lepidota* Nutt. (III), July 15 (*1139*).

UROMYCES HEDYSARI-OBSCURI (DC.) Car. & Picc. Camp Davis: on *Hedysarum cinerascens* Rydb. (I), June 17 (*1010*). Hoback Canyon: on *Hedysarum* sp. (I, II & III), Granite Creek, Aug. 1 (*1192*). South of Teton Pass: on *Hedysarum* sp. (I), July 11 (*1125*).

UROMYCES PLUMBARIUS Peck. Gros Ventre River: on *Pachylophus caespitosus* (Nutt.) Raim. (III), July 19 (*1161*).

UROMYCES SOLIDAGINIS (Sommerf.) Niessl. Hoback Canyon: on *Solidago* sp. (III), Granite Creek, Aug. 1 (*1196*). These host leaves were originally designated as *Aster*, but are probably from a broad leaved species of *Solidago*, as the teliospores fit this species of *Uromyces* very well.

HYMENOMYCETES

Exobasidium Vaccinii (Fck.) Woron. Teton National Park: Indian Paint Brush Canyon, on *Menziesia ferruginea* Smith, July 30 (*1187*) and *Vaccinium membranaceum* Dougl., July 30 (*1257*).

Sarcodon imbricatus (L.) Karst. Teton National Park: on stream

bank, Indian Paint Brush Canyon, July 30 (*1271*). *Fomes Pini* (Thore) Lloyd. Hoback Canyon: on conifer log, Red Creek, July 29 (*1273*). *Polyporus borealis* Fr. Teton National Park: on conifer log, Indian Paint Brush Canyon, July 30 (*1272*). *Coprinus ephermerus* Fr. Hoback Forest Camp: on horse dung, July 22 (*1235*). *Inocybe eutheles* (B. & Br.) Quél. Teton National Park: on mosses, Indian Paint Brush Canyon, July 30 (*1236*). *Inocybe rimosa sensu* Kauffman. Hoback-Snake-River-Junction, on moist bank, July 17 (*1237*). *Lactarius deliciosus* (Fr.) Quél. Hoback Forest Camp: under shrubs, July 22 (*1238*). *Lactarius Hibbardiae* Pk. Teton National Park: under spruce, Indian Paint Brush Canyon, July 30 (*1239*). *Panaeolus retirugis* (Fr.)Quél. Hoback Forest Camp: on horse dung, July 22 (*1240*). *Panaeolus semiovatus* (Fr.) Lundell. Hoback Forest Camp: on horse dung, July 22 (*1241*). *Pholiota squarrosa* (Fr.) Quél. Hoback Forest Camp: on rotten log, July 22 (*1242*). *Pleurotus striatulus* (Fr.) Quél. Hoback Canyon: on decayed conifer wood, July 17 (*1243*). *Psilocybe coprophila sensu* Ricken. Hoback Forest Camp: on horse dung, July 22 (*1244*). *Psilocybe sarcocephala* (Fr.) Gill. Hoback Forest Camp: on old wood, July 17 (*1245*). *Russula chamaeleontina sensu* Kauffman. Jackson, Wyo. (*1246*). *Stropharia semiglobata* (Fr.) Quél. var. *stercoraria*. Hoback Forest Camp: on horse dung, July 22 (*1234*).

FUNGI IMPERFECTI

A few collections of this group of fungi which have turned up since the earlier papers were published are considered here.

DIDYMARIA CONFERTA Syd.

This fungus forms angular brown areas between the smaller veins on both sides of the leaves. Two types of pustules, both arising from an interwoven knot of hyphae, are formed. In the case of the *Didymaria* pustules, the epidermis is widely ruptured and a dense fascicle of short stout conidiophores, 35–44 × 5–7 μ, is erumpent through it. These conidiophores bear oblong-ellipsoid, two-celled, hyaline conidia with a flattened basal scar and they measure 26–32(35) × 9–12.5 μ. The second type of pustule results from the formation of a spherical mass of hyphae with a defi-

nite outer dark brown wall and a radiate internal arrangement of hyphae. No spore formation was seen in any of these. They appear as minute black sclerotial dots, which may be either immature perithecia or pycnidia, and are very abundant in this material.

Hoback Canyon: Granite Creek, on *Wyethia amplexicaulis* Nutt., Aug. 1 (*1255*).

This fungus appears to be the same as that reported by Solheim (**15**, IV: 44) under this name, and upon examination of material sent him, Dr. Solheim (*in litt.*) states that they are identical and that his material also shows a few of the sclerotial bodies. This species was described (**16**, p. 186) from a collection by A. O. Garrett, on the same host, from Utah, and a later collection by Garrett (Fung. Col. *4723*) from the same host and locality is identical with the above collection and also shows a few sclerotial bodies.

In 1894, however, Ellis (**5**, p. 373) described a *Marsonia Wyethiae*, on *Wyethia glabra*, from California. An examination of type material (N.A.F. *3184*) of this species shows that it is very similar to if not merely a variety of *Didymaria conferta*. This *Marsonia* shows the same angular spots, but not the black sclerotial bodies. The acervuli are yellow-brown rather than pinkish-tan or grey, as in *D. conferta*, and the spores are shorter and more ovoid (20–23 × 10–13 μ). The spores in Fung. Col. *4723* are quite variable (18–27 × 10–13 μ), but generally more cylindric.

Didymaria is supposed to be one of the Moniliales, but these species have a definite basal stromatic cushion in the host. On the other hand they break through the epidermis freely and have freely exposed conidiophores. What is to determine the limits of these and neighboring genera, and thereby the proper binomial can only be decided by a comparative study of a large group of related species.

Cylindrosporium Umbelliferarum nom. nov.

Ascochyta Heraclei Lib. Exs. No. *51*.
Septoria Heraclei (Lib.) Desm. Pl. cr. Nord. d. Fr. No. *534*.
Cylindrosporium Heraclei E. & E. Journ. Myc. **4**: 52. 1888.
Cylindrosporium Heraclei (Lib.) Höhn. Sitz. Akad. Wiss. Wien **115**: 28. 1906.
Phlocochora Heraclei (Lib.) Höhn. Ber. deutsch. bot. Ges. **35**: 253. 1917.

Upper leaf surface only slightly differentiated or with numerous slightly discolored, small, angular areas, 1–2 mm. across, limited by the smaller veins. Under side of leaf with numerous small, flat, pulvinate, often confluent, black stromata, 200–800 μ in diameter and 150 μ thick.

Acervuli mostly epiphyllous, sometimes hypophyllous, arising as a thin stromatic layer, 400–800 μ in diameter, just beneath the epidermis. Hymenial layer of short fine conidiophores, causing a rupturing of the epidermis and a pushing out of a light colored mass of conidia, which are long, cylindric or somewhat tapered at the ends, more or less strongly curved, uniseptate, and 35–48 $\times$ 3.5 μ.

The stromata on the under surface are thickly scattered, dothideaceous, and composed of dark, thick-walled pseudoparenchyma. They rupture the epidermis and often show globose locular areas of lighter colored cells, but no asci or spores were seen. They appear to be the ascus stage of some dothideaceous fungus.

Hoback Canyon: on *Heracleum lanatum* Michx. Granite Creek, Aug. 1 (*1254*) and Forest Camp, July 22 (*1258*).

This fungus is the same as Ellis' *Cylindrosporium Heraclei* (**4**) (N.A.F. *3181*), of which he says "with *Phyllachora Heraclei* (Fr.)." Solheim (**15**, IV), in reporting this species, on *Ligusticum*, gives the conidia as 50–101 $\times$ 3–3.5 μ and says "The fungus is frequently associated with immature perithecial bodies." A collection made by Kauffman & Kanouse, at Centennial, Wyoming (Univ. Mich. Crypt. Herb.), shows similar stromatic bodies and acervuli. European collections (*i.e.* Krieger, Fung. Sax. *1597*) show an association of the same acervuli and conidia with similar stromatic bodies. Sydow's Myc. Germ. *1277*, of *C. Heraclei* (Lib.) Höhn., on *Pastinaca sativa*, on the other hand, shows this same type of acervulus and conidium, but no sclerotial bodies whatever. Although there is a good deal of variation in the size and character of the spots and acervuli and the size of the stromatic bodies and length of the conidia, there appears to be no correlation between these and the host or region. The spores all show the characteristic form and septation, and this association seems to be a widely distributed one on the Umbelliferae. Saccardo (Syll.

Fung. **2**: 600) gives *Septoria Heraclei* (Lib.) Desm. as the spermogonial stage of *Phyllachora Heraclei* and Magnus (**10**) states that he has found the *Phyllachora* stage associated with Ellis' fungus, *C. Heraclei.*

There are a large number of conidial stages in the form genera *Cylindrosporium, Septogloeum, Ramularia, Phloeospora, Rhabdospora, Ascochyta,* etc., described on various species of the Umbelliferae, with conidia similar to those of this collection. There is so much ambiguity in the descriptions, however, that only an examination of authentic material can determine the true position of most of them. Höhnel (**8**), following Magnus (**10**), unites *Septoria Heraclei* (Lib.) Desm., *Cylindrosporium Heraclei* E. & E. and *C. hamatum* Bres. under the binomial *Cylindrosporium Heraclei* (Lib.) Höhn. In 1917, Höhnel (**9**) published a name, *Phloeochora,* which he applied to the conidial stages of species of *Phyllachora* (*Oligostroma*) occurring on Umbellifers. He gave the generic character merely as "Ähnlich *Phloeospora* aber phyllachoroid," and made the combination *P. Heraclei* (Lib.) Höhn. Even if this were considered a tenable generic description, it is obvious that his fungus is not like a *Phloeospora,* for it was separated from such forms by Magnus (**10**) who states that no *Septoria*-like forms were found in connection with *Phyllachora,* and Höhnel (**8**), himself, says of this fungus "Gehause fehlend." If this name is rejected, the fungus falls in *Cylindrosporium,* where it properly belongs. Unfortunately, however, both the binomials *Cylindrosporium Heraclei* (Lib.) Höhn. and *C. Heraclei* E. & E. (which becomes a synonym) are preceded by the prior *C. Heraclei* Oud. (**12**). Saccardo placed Oudemans' species as *Ramularia Heraclei* (Oud.) Sacc. Oudemans gave the spores as merely 12–25 × 4–5 μ. Saccardo gave them as 23–30 × 4–7 μ, fusoid, 1–3 septate and on long filiform conidiophore hyphae, 50–60 × 2–3 μ, which would indicate a different species from the one here discussed. It is necessary, therefore, to change the species name, and *C. umbelliferarum* is used. *Fusoma Heraclei* Oud. (**13**), with conidia 45–60 × 4 μ, finally septate and curved may be the same as *C. Umbelliferarum.*

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ANALYSIS OF PECK'S TYPES OF *MELIO LA BALSAMICOLA* AND *ASTERINA NUDA*

GLENN GARDNER HAHN *

(WITH 2 FIGURES)

About sixteen years ago Gäumann (**3**) directed the attention of forest pathologists to a new and outstanding needle disease of Douglas-fir, *Pseudotsuga taxifolia* (Poir.) Britt. in Europe. In his announcement he suggested that the parasite involved might possibly be identical with an old fungus, *Adelopus balsamicola* (Peck) Theiss. (**19**, p. 482), an innocuous organism occurring commonly on the dead needles of balsam fir (*Abies balsamea* [L.] Mill.) in the United States. Gäumann (**3**, p. 66) stated the taxonomical problem as follows: "So far as the observations herein presented are concerned our fungus . . . is an ascomycete belonging to the genus *Adelopus*. According to our knowledge, a single species is known in this genus, namely, *Adelopus balsamicola* (Peck) Theiss. This species, which Wilson and Waldie (1928) investigated recently, was described originally in the year 1881 by Peck as *Meliola balsamicola* on the needles of *Abies balsamea* in the United States. Four years later Peck described the same fungus once more under the name *Asterina nuda*. Again eight years later the fungus was allocated by Ellis and Everhart to *Dimerosporium balsamicolum*. . . . Whether the form growing on Douglas-fir is identical with the original *A. balsamicola* growing on *Abies* needs demonstration by further research."

Following Gäumann's paper a considerable number of publications, all foreign, dealing with *Adelopus* appeared in the years preceding the outbreak of the war in 1939. Those by Plassmann (**14**), Steiner (**17**), and Rohde (**15**) particularly dealt with the taxonomic confusion of the organisms involved. Rohde recognized the Douglas-fir needle parasite definitely as a new species,

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which he called *Adelopus Gäumanni* in honor of the Swiss phytopathologist. At the same time he (**15**, pp. 495–498) analyzed the accumulated literature pertaining to the taxonomic relationship of the much discussed *Meliola balsamicola* (**10**) and *Asterina nuda* (**11**). For the first time this relationship appeared to be clarified correctly despite the fact that Rohde did not examine Peck's types.

In the study reported here, Peck's types and ten subsequent collections[1] relating to them have been examined. Some of the Albany material had been annotated by Dearness and two specimens had been determined by Saccardo. The writer also examined numerous fresh American specimens of Peck's *Asterina nuda*. In the main the writer's findings confirm Rohde's (**15**) conclusions; in addition, they present new and unpublished morphological data.

PECK'S TYPES AND OTHER HERBARIUM SPECIMENS

A study of Peck's types showed that *Meliola balsamicola* and *Asterina nuda* are two very distinct species. It confirmed Peck's (**10**, p. 52; **11**, p. 102) original descriptions as well as his figures, which indicate definitely that Peck had intended originally to erect two species in two different genera.

MELIOLA BALSAMICOLA Pk. 1881

The label of the type packet carries the printed name, "*Asterina balsamicola* Pk.," a name that was never published. It is not known who printed this name. Although the collection date is not given, the year of collection according to a written communication from House (February 15, 1943) is the year for which the report is made. It appears that Peck did not date his collections

[1] Through the courtesy of Dr. H. D. House, State Botanist, the writer was permitted to examine and study Peck's types and other related material deposited at the New York State Museum, Albany, N. Y.

FIG. 1. Peck's types, *Meliola balsamicola* and *Asterina nuda* on *Abies balsamea* needles. *A*, Perithecia of *M. balsamicola* on the upper surface of a needle associated with an apothecium of *Peziza balsamicola*. × 36. *B*, Perithecia of *A. nuda* arising from the stomata on the under side of the needle. × 36. *C*, Young subiculum of *M. balsamicola* showing coarse brown, applanate filaments on the upper side of the needle. × 36. *D*, Enlarged perithecia of *A. nuda*. × 72.

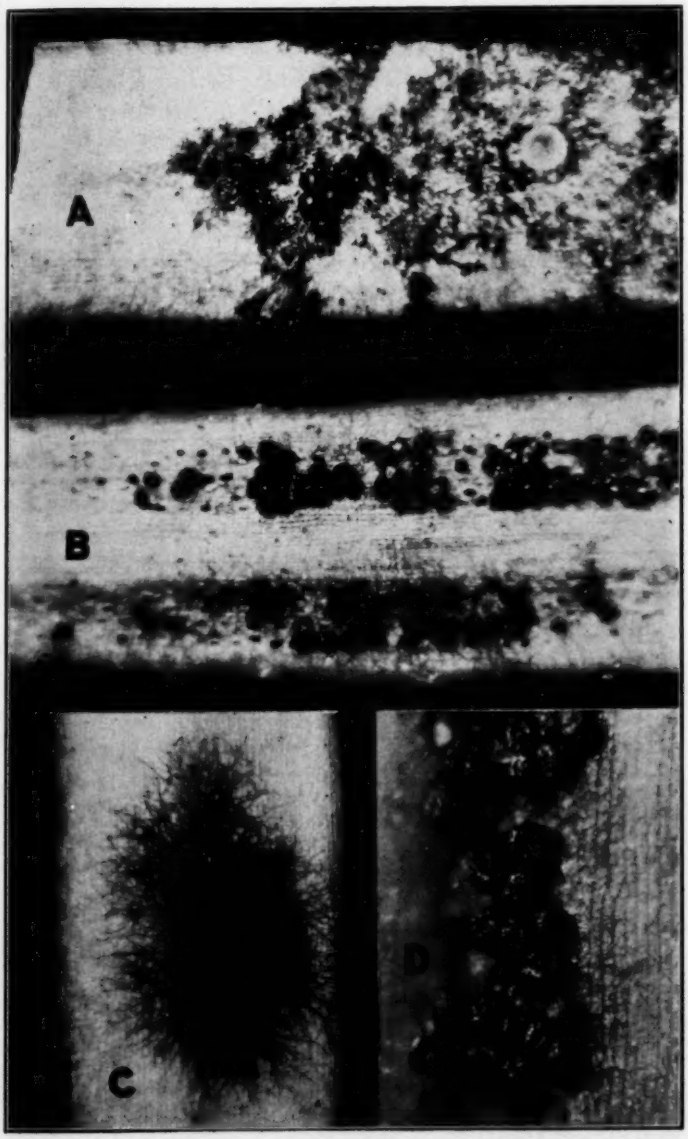

FIG. 1.

as a rule, and he rarely published a new species, except in his yearly report. In what appears to be Peck's handwriting the following data are also given: "Leg. Chas. H. Peck," and below *"Asterella"* and *"(Meliola balsamicola* Pk.)." The parentheses about *M. balsamicola* were very probably not placed there by Peck but by someone else. Apparently at the time Peck wrote the label in part, he was uncertain as to what he was going to call his fungus; however, he (**10**, p. 52) published it as *Meliola*.

The majority of the needles in the type collection show the *Meliola* described and illustrated by Peck (**10**, p. 52; Pl. I, FIGS. 23–27). As he pointed out the perithecia are exceedingly *few* in number (FIG. 1, *A*).[2] In this the species differs markedly from *Asterina nuda*, which produces an abundance of closely crowded fruiting bodies (FIG. 1, *B;* **15**, FIG. 8). The writer observed the perithecia of *Meliola balsamicola* as being smooth, superficial, separate or clustered, blackish, ovate or subconical, mostly epiphyllous, less commonly hypophyllous, seated on an irregularly radiating, dark brownish, patchlike subiculum. This subiculum, which is very conspicuous, is at first applanate and filamentous (FIG. 1, *C*) but as the colony develops it becomes crustaceous (FIG. 1, *A*). In addition to differences in perithecial production (FIG. 1, *A, B*), the superficial subiculum sets off distinctly the *Meliola* from *A. nuda* with its intramatrical mycelial development. Rohde (**15**, p. 498) noted that in Peck's illustrations the perithecia of *M. balsamicola* are shown as being larger than those of *A. nuda*. Peck did not record measurements of perithecia for his species nor did the writer measure any in the type. A comparison of the fruiting bodies of the two species shown (FIG. 1) indicates that those of the *Meliola* are the larger, but Peck (**10**, Pl. 1, fig. 23) exaggerated their size in his illustration. The writer made no measurements of asci or of the bilocular ascospores. The spore size recorded by Peck of 9–11 μ has remained unaltered in the literature, although Saccardo referred the fungus without a new description to *Zukalia?* in 1891, and Ellis and Everhart placed it in *Dimerosporium* the following year. The writer observed that the ascospores recorded

[2] The writer is grateful to Dr. R. P. Marshall for the photomicrographs reproduced in this figure and to the late Dr. L. O. Overholts for the one given in fig. 2.

by Peck as being hyaline become fuligineous. Paraphyses were not reported by Peck nor were they observed by the writer.

Peck reported the type of *Meliola balsamicola* as being associated with *Peziza* (*Tapesia*) *balsamicola* n. sp. on "living or languishing leaves of balsam fir." A single apothecium of the latter is shown in FIG. 1, *A*. Three needles were also observed showing the perithecia of Peck's other species, the much discussed *Asterina nuda*. The latter fungus is so commonly distributed that it was not surprising to find some of it in needle collections of the *Meliola*. The type specimen of *P. balsamicola*, which was also examined, contains material of the *Meliola* and it was in this material rather than in the type of *M. balsamicola* that the writer found the olive-brown, bilocular ascospores. The writer examined perithecia on only a very few needles of the type specimen but undoubtedly mature colored spores are to be found in it.

ASTERINA NUDA Pk. 1885

On the type packet Peck wrote the name, *Asterina nuda*, which was reported both by himself (**11**, p. 102) and Martin (**7**, p. 134) in 1885. Later in 1909 when a list of species and varieties of fungi described by Peck (**12**, p. 65) appeared, the same name, *A. nuda*, was used with a single synonym, *Asterella nuda* Sacc. The type collection, which is not a large one, consists of needles that were dead at the time of collection. In it, among others, is an organism commonly present, which Peck undoubtedly intended as his *Asterina nuda* (FIG. 1, *B, D*). Material of *Meliola balsamicola* is not present. Perithecia of *A. nuda* on two needles were examined. As described by Theissen (**18**, pp. 72–73), Steiner (**17**), and Rohde (**15**), all of whom examined American material of the species, the fruiting bodies are distributed linearly along the stomatal openings, mostly on the lower (FIG. 1, *B*), but also on the upper needle surfaces where stomata likewise occur. In their dry condition the fully mature perithecia appear as if lacquered. They are tenacious, leathery, dull-shining, coarsely granular, becoming flattened cakelike and umbilicate, the elliptical ones having a deep, irregular suture (FIG. 1, *D*). The perithecia (FIG. 2) are formed superficially from well developed "stalks" arising from the stomata. The stalks are connected with what may be called "basal plates"

of interwoven hyphae in the parenchyma tissue of the needle (**15**, FIG. 10; **17**, FIG. 12). The bilocular ascospores within the asci are hyaline, but occasional free, olive-brown ones are to be found. Paraphyses, which were not recorded by Peck, were not observed.

In fresh material of the species, an important unreported morphological development preceding ascospore discharge was observed. Before spore ejection, the sheath of the endoascus becomes elongated as a slender "clamlike" neck, at times becoming approximately as long as the ascus. As this inner sheath is extended, the walls of the ascus shrink in width so that the sheath appears as a tubular structure with a somewhat narrower necklike prolongation. These endoascus extensions that have been emptied of their spores persist as tubular sacs and are faintly but unmistakably discernible. The writer also observed them to be present in Peck's type.

In addition to the type and fresh material of *Asterina nuda,* the following specimens of it were studied; some had been incorrectly determined and all but one were collected in New York State:

(1) *Asterina nuda* Pk. Sandlake. Coll. Peck, June.
(2) *Asterella nuda* (Pk.) Sacc. N. Elba. Coll. Peck, June–Sept.
(3) *Asterina nuda.* Bathurst, N. B. Coll. Richards, July, 1892 (Herb. W. G. Farlow).
(4) *Dimerosporium balsamicola* (Pk.) Ell. & Ev. N. Elba. Coll. Peck, June, 1911 (det. Sacc.).
(5) *Dimerosporium balsamicola* (No. *1454*). Tupper Lake. Coll. House, Aug., 1913 (det. Sacc.).
(6) *Dimerosporium balsamicola* Newcomb. Coll. House, June, 1921.
(7) *Asterina nuda.* Newcomb. Coll. House, June, 1922.
(8) *Asterina nuda.* North Creek. Coll. House, June, 1923.
(9) *Dimerosporium balsamicolum.* Tahawas. Coll. House, June, 1923.
(10) *Asterina nuda.* Lake Sanford. Coll. House, Aug., 1924 (det. Dearness).

The 1911 and 1913 specimens of *Asterina nuda* mentioned, which were determined incorrectly by Saccardo (**16**, p. 115) as *Dimerosporium balsamicola,* have mostly hyaline or dilutely colored two-celled ascospores within the asci. Free olive-brown or sooty brown ascospores are also encountered. Only occasionally did the writer observe swollen, nonextended asci with brown spores. In one instance (specimen no. *1454*) an elongated discharging ascus was noted containing three colored bilocular spores

at the base of the sac. The walls of this sac had shrunken in width to form a tubular structure, the upper part of which was elongated, and the extension of the endoascus contained one sooty brown spore. Although brown ascospores were readily evident to the writer and Dr. A. M. Waterman, who at the writer's request independently corroborated some of his observations, they were not observed by Saccardo (**6**, p. 46; **16**, p. 115).

Colored ascospores that become sooty brown upon full maturity are to be found likewise in the Sandlake, Newcomb, Tahawas, and Lake Sanford collections listed above. Dearness annotated the Lake Sanford specimen packet as follows: "I think this is Peck's *Asterina nuda* although I failed after trials on three different twigs to get asci and spores." The extended empty endoasci described previously are present moreover in the Sandlake, Newcomb, and Tahawas material.

TAXONOMICAL DISCUSSION

A consideration of the foregoing morphological data regarding *Meliola balsamicola* and *Asterina nuda* makes it difficult to understand how some mycologists could confuse the two species. In 1892 Ellis and Everhart (**2**, pp. 35, 36) had recognized the separate identities of Peck's two species when they published his *Meliola* as *Dimerosporium balsamicolum* despite Peck's (**10**, p. 52) opinion of 1881 that: "Our fungus does not fully meet the requirements of the genus *Meliola*, neither is it a good *Asterina* nor *Dimerosporium*. It needs further investigation." Twenty-eight years later Peck (**12**, pp. 65, 129) relisted his *Meliola* and *Asterina* species separately, but failed to take cognizance of the change Ellis and Everhart had made in the name of the former controversial fungus. Subsequently Saccardo (**16**, p. 115) caused considerable confusion when he united the two species under *D. balsamicola*.

Preliminary observations made by the writer upon which a further study of *Meliola balsamicola* may be based, indicate that it belongs to the Perisporiaceae (Phaeodidymae) and probably in the genus *Dimerium* Sacc. & Syd. This genus contains the interesting parasite, *Dimerium Juniperi*, described by Dearness (**1**, p. 244) as a new species with small, dark, crustaceous subicula

strikingly seated in association with resinous glandular pits on the middle of the back of green leaf scales of *Juniperus occidentalis* Hook. (California).

The type specimen of the parasite, *Meliola balsamicola,* and material of it in the type collection of *Peziza* (*Tapesia*) *balsamicola,* are the only specimens known to the writer. Although parts of Peck's type of *P. balsamicola* possibly containing *M. balsamicola* have been deposited at the New York Botanical Garden, part of the *Meliola* type is not present there. One wonders whether *M. balsamicola* is a rare fungus in contrast with the much investigated *A. nuda,* which occurs commonly and abundantly over wide areas in North America and sparsely in Europe on a number of *Abies* spp.

Over a period of more than fifty years *Asterina* (*Adelopus*) *nuda* has been studied by a number of our leading mycologists. However, colored ascospores, which are so characteristic of the species when it is fully mature, were not observed by any of them. In this regard it should be remarked that Waldie wrote on March 31, 1927 to Professor J. S. Boyce, Yale University, New Haven, Conn., commenting on spore coloration in *A. nuda* as follows: "I wonder if . . . brown color might not develop at a very late stage. . . . It is worth watching for." Wilson and Waldie (**20**: 152–153) apparently did not succeed in finding dark spores. Petrak (**13**) also speculated on spore coloration but unfortunately appropriate material of *A. nuda* was not at hand to enable him to make this observation.

Because of a general interest in *Adelopus* (*Asterina*) *nudus* and the uncertainties concerning its name, the species has inherited an involved synonomy. Dearness aptly described the situation in an informative letter to the writer on September 14, 1941: "It makes me happy to think you are seriously attacking *Adelopus* on conifers. . . . I have perspired over the (?) synonomy of what I take to be *Adelopus* alias *Dimerosporium balsamicola*. . . . Have you referred the following names to their proper place?" Therewith he listed a long series of names and added a little sketch of an *Adelopus* perithecium with its hidden or secret (adelo, αδηλο) foot or stalk (pus, πους). The writer's interpretation of the relationship of the binomials involved is as follows:

ADELOPUS NUDUS (Peck) Hoehn. Sitzb. Akad. Wiss. Wien, math.–nat. Kl. **127** (1): 619. 1918.

Asterina nuda Pk. 38 Ann. Rpt. N. Y. St. Mus. Nat. Hist., p. 102. 1885.
Asterella nuda Sacc. Syll. Fung. **9**: 397. 1891.
Cryptopus nudus Theiss. Ann. Mycol. **12**: 72. 1914.
Adelopus balsamicola Theiss. Ann. Mycol. **15**: 482. 1917.
? *Phaeocryptopus nudus* Petr. Ann. Mycol. **36**: 14. 1938.

DIMEROSPORIUM BALSAMICOLA (Pk.) Ell. & Ev. North Am. Pyr., p. 728. 1892.

Meliola balsamicola Pk. 34 Ann. Rpt. N. Y. St. Mus. Nat. Hist., p. 52. 1881.
Asterina balsamicola Pk., in herb. (on label of type packet).
Zukalia ? balsamicola Sacc. Syll. Fung. **9**: 432. 1891.

The combination *A. nudus* (Pk.) Hoehn. is preferred for the species rather than *A. nudus* (Pk.) Theiss. published by von

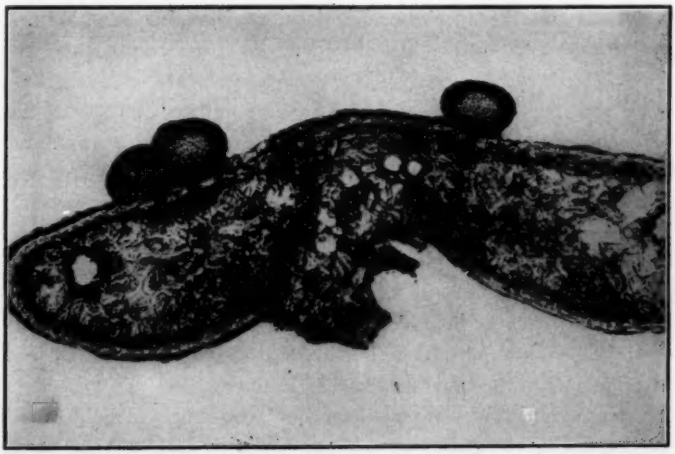

FIG. 2. Perithecia of *Adelopus nudus* on dead needle of *Abies balsamea*. × 95.

Hoehnel (**5**: 617–619), who gave "Theiss." rather than himself as author. In adopting the former combination, which is in accordance with International Rules, the writer has followed Petrak (**13**:

10, 15) rather than Rohde (**15**), who used the combination published by von Hoehnel.

As will be noted, the synonymity of *Adelopus* (1917) with *Phaeocryptopus* (1914) is questioned. In an extensive paper Petrak (**13**) gave reasons in favor of synonymity but unfortunately they are not based on an examination of the type, *Phaeocryptopus Abietis* Naoumoff (**8**, p. 424; **9**, p. 20) collected on needles of *Abies sibirica* Ledeb. from the Ural Mts., Siberia. Moreover, Petrak did not study American material of *Adelopus nudus*. The perithecia of both genera appear to resemble each other closely and they are evidently formed in the same manner. Those of *Phaeocryptopus*, however, are reported as being paraphysate (**8**, pl. 32, fig. 2; **9**, p. 20) whereas paraphyses are definitely lacking in *Adelopus*. Theissen (**18**), von Hoehnel (**4**: 265–266, **5**), Wilson and Waldie (**20**), and Rohde (**15**) have all reported on the absence of these structures. Their observations confirm those made by the writer and Waterman, who has made a considerable number of examinations of *nudus* material. On the other hand Wilson and Waldie (**20**) when they recorded *nudus* in Scotland also reported *P. Abietis* on needles of herbarium specimens of *A. Faxoniana* Rehd. & Wils., collected in N. W. Yunnan, China. In the latter they described the occurrence of filiform, hyaline paraphyses, $70 \times 2.5\ \mu$; those reported by Naoumoff were similar in shape and size. The writer has been unable to study material of Naoumoff's *P. Abietis* for it is lacking in American herbaria.

The classification of *Adelopus* (= *Cryptopus*) Theiss. (**18**: 72–73) based on the species *Adelopus nudus* in the Capnodiaceae (Hyalodidymae) as indicated by Petrak (**13**: 12–13) is questionable. This study has shown that colored ascospores are produced by *nudus*. On the other hand, only hyaline spores are formed in the new species, *A. Gäumanni*, as has been amply demonstrated by the intensive studies of Steiner (**17**), Rohde (**15**), Petrak (**13**), and those of the writer as yet unpublished. Our concept of *Adelopus*, therefore, must be broadened to include species with colored as well as hyaline spores.

SUMMARY

For the first time since the days of Peck, his two type specimens, *Meliola balsamicola* 1881 and *Asterina nuda* 1885, both collected on *Abies balsamea* (L.) Mill., have been studied. Results show that these two organisms regarded as synonymous by Saccardo, who studied American specimens of *A. nuda,* are not only distinct species as Peck stated, but also belong to different genera.

Meliola balsamicola, a little known and rarely collected species on green balsam fir needles, does not belong either to *Meliola,* or to *Dimerosporium* where Ellis and Everhart placed it. It belongs to the Perisporiaceae (Phaeodidymae) and probably in the genus *Dimerium;* additional collections as well as an intensive study of it are needed.

Asterina nuda, a common fungus on dead fir needles, has been investigated extensively abroad for many years. The name preferred for the fungus, the involved synonomy of which is discussed, is *Adelopus nudus* (Pk.) Hoehn.

New morphological data for both species are given.

DIVISION OF FOREST PATHOLOGY,
BUREAU OF PLANT INDUSTRY,
SOILS AND AGRICULTURAL ENGINEERING
IN COÖPERATION WITH
THE OSBORN BOTANICAL LABORATORY,
YALE UNIVERSITY,
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NOTES AND BRIEF ARTICLES

MYCOLOGICAL SOCIETY OF AMERICA

REPORT OF THE 1946 FORAY

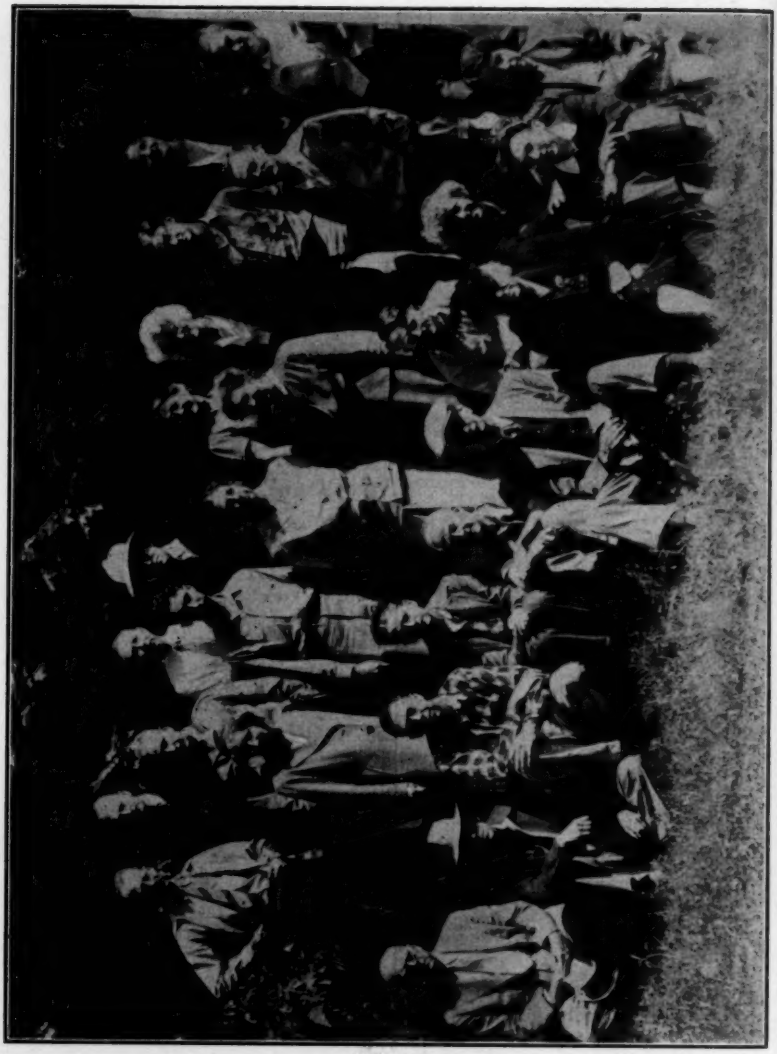
(WITH 1 FIGURE)

At the twelfth annual meeting of the Mycological Society of America at St. Louis in March 1946, it was directed that the mycological summer forays, long one of the popular activities of the Society, be resumed. The invitation, extended to the Society by Dr. C. R. Orton, Dean of the College of Agriculture and Director of the Agricultural Experiment Station of the University of West Virginia, on behalf of himself and his colleagues in the Department of Plant Pathology, to hold the first of the new series of forays in his State was accepted. The Southern Appalachian Botanical Club participated.

Headquarters were established in the laboratories of the Plant Pathology Department where facilities were available for arranging, drying and studying collected material. Dr. H. L. Barnett served very efficiently as local chairman and guide for the collecting parties. The group assembled at Morgantown on the afternoon of August 29 and left the following morning for Cheat Bridge and vicinity in Randolph County, collecting there in the afternoon and at two points along Route 250, north of Elkins, en route.

The night was spent at Elkins, where Dr. Ernst Bessey entertained with reminiscences of early collecting days in Colorado. Activities on the second day included a visit to Blackwater Falls State Park and collecting south of Davis and at a point on Route 219 just within the boundaries of Preston Co. The day was to have been concluded with a tour of the famous Cranesville Glades, but there appears to be reasonable doubt as to whether anyone but Dean Orton actually reached the Glades.

About thirty people, including the local group, were in attendance. Continued dry weather had limited very definitely the num-



The Mycological Society's foray, West Virginia, Sept. 1, 1946. *Photograph by H. L. Barnett*

ber of fungi available, particularly of fleshy forms, but nevertheless an enjoyable as well as worthwhile time was had by all participating.

Sunday morning, September 1, was given over to study and care of collections. There was also available for inspection at this time a series of carefully prepared exhibits covering some of the work in mycology and plant pathology of staff members. The visitors were entertained later in the day by an informal gathering and picnic supper at Chestnut Ridge camp, a few miles out of Morgantown. Local collecting was the order of the day on Monday, followed in the evening by a most pleasant get-together at the home of Dean and Mrs. Orton.

The thanks of the Society have been extended to Dean Orton and his associates for the many and varied efforts put forth to make the foray a success.—JOHN A. STEVENSON.

BOOKS AND WORLD RECOVERY

The desperate and continued need for American publications to serve as tools of physical and intellectual reconstruction abroad has been made vividly apparent by appeals from scholars in many lands. The American Book Center for War Devastated Libraries has been urged to continue meeting this need at least through 1947. The Book Center is therefore making a renewed appeal for American books and periodicals—for *technical and scholarly books and periodicals in all fields* and particularly for *publications of the past ten years*. We shall especially welcome complete or incomplete files of MYCOLOGIA.

The generous support which has been given to the Book Center has made it possible to ship more than 700,000 volumes abroad in the past year. It is hoped to double this amount before the Book Center closes. The books and periodicals which your personal or institutional library can spare are urgently needed and will help in the reconstruction which must preface world understanding and peace.

Seated, L. to R.—H. M. Fitzpatrick, M. B. Walters, J. B. Routien, Mrs. Routien, E. A. Bessey, C. L. Shear, J. A. Stevenson, Mrs. Shear, Miss Walters, Miss Ryan, Miss Hayes. Standing, L. to R.—H. L. Barnett, W. W. Diehl, Mrs. Fitzpatrick, J. G. Leach, R. W. Davidson, C. T. Rogerson, J. G. Brown, Miss Cash, Mrs. Dayton, Mrs. Stevenson, W. L. Dayton, Mrs. Walters, Mr. Mozingo, L. K. Henry, Miss Dayton.

The Mycological Society's foray, West Virginia, Sept. 1, 1946. *Photograph by H. L. Barnett*

Ship your contributions to the American Book Center, c/o The Library of Congress, Washington 25, D. C., freight prepaid, or write to the Center for further information.—A. H. SMITH.

A NEW COMBINATION FOR BRUNCHORSTIA GIBBOSA

Recently there has come to the writer's attention a doctorate dissertation [1] dealing with *Crumenula* on pine. This monographic paper is of particular importance to forest pathologists in this country where the genus *Crumenula* with its imperfect stage, *Brunchorstia* Eriks., is little known. It includes a discussion,[1] pp. 66–68, of the new species, *Brunchorstia gibbosa* Wr., which Wollenweber,[2] pp. 498–499, published in 1931 after he had received material from the writer for identification. This material had been collected originally by Dr. J. S. Boyce, Yale University, New Haven, Conn., on cankers of Douglas-fir [*Pseudotsuga taxifolia* (Poir.) Britt.] near North Bend, King Co., Washington, in 1927 and had been sent for examination to the writer, who at the time was investigating Douglas-fir cankers in Great Britain. Boyce also sent some of this canker material to Dearness for his opinion. In 1928 Dearness described [3] the North Bend specimen (Herb. J. S. Boyce *1285, 1766;* collections for study, U. S. Div. Forest Pathology, *40,394;* Herb. Dearn. *5666*) as the new species, *Cryptosporium Boycei.*

A consideration of the genus *Cryptosporium* Sacc. would serve to indicate that the Boyce fungus does not belong there. The species should now be known as **Brunchorstia Boycei** (Dearn.) comb. nov. with *B. gibbosa* and *Cryptosporium Boycei* as synonyms. Ettlinger grew in culture what he regarded as a European isolate of *B. gibbosa* (= *Boycei*) (from *Abies alba* Mill.) and compared its characters with those of *B. pinea* (Karst.) Hoehn. (= *Crumenula abietina* Lgbg.[1]) and *B. laricina* Ettlinger (= *Crumenula laricina* Ettlinger [1]). He stated that the characters of this

[1] Ettlinger, L. Über die Gattung *Crumenula* sensu Rehm mit besonderer Berücksichtigung des *Crumenula*-Triebsterbens der *Pinus*-Arten. Beitr. Kryptogamenflora Schweiz **10**: 1–73. 1945. (Bot. Abs. **20**: 13397. 1946.)

[2] Wollenweber, H. W. *Fusarium*-Monographie. Fungi parasitici et saprophytici. Zeitschr. f. Parasitenkde. **3**: 269–512. 1931.

[3] Dearness, J. New and noteworthy fungi—V. Mycologia **20**: 235–246. 1928.

fungus were so different from those of the two other species that he doubted a relationship between it and *Crumenula*. It would be interesting to compare the cultural characters of the isolate from *A. alba* with those of the species isolated from Douglas-fir in the United States.—GLENN GARDNER HAHN.

NOTICE

It has been called to our attention that beginning with Volume 10, 1947, the TAXONOMIC INDEX, a publication of the American Society of Plant Taxonomists, will include a section on the systematics of the fungi. All those interested in receiving this service may communicate with the Editor, W. H. Camp, New York Botanical Garden, New York 58, N. Y.—A. H. SMITH.

NOTICE

For a number of years past, the early volumes of MYCOLOGIA (Vols. 1–24 plus index) have been selling under our special offer of $50.00, much below the original cost of printing. Because of dwindling stock it will be necessary to withdraw this offer after July 1, 1947, and offer these at the regular publication price indicated on the covers.—FRED J. SEAVER.